Probing the foundations of comparative cognition: the structure, stability and predictability of great ape cognition

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Abstract

Theories in psychology, cognitive science, anthropology and evolutionary biology use great ape cognition as a reference point to specify the evolutionary dynamics that give rise to complex cognitive abilities and to define the nature of human cognition. This approach requires a comprehensive way of describing great ape cognition to compare it to other primates – including humans. Empirically, this entails that a) group-level results are measured stably, b) individual differences are measured reliably, and c) cognitive performance is predictable. The study reported puts these assumptions to a test. We repeatedly tested a large sample of great apes in five tasks covering a range of cognitive domains. Group-level performance was relatively stable, so different testing occasions licensed the same conclusions. Most of the tasks showed high re-test correlations and were thus suited to study individual differences. Individual differences in performance were explained mainly by stable differences in cognitive abilities between individuals. Furthermore, we found systematic relations between cognitive abilities. Finally, when predicting cognitive performance, we found stable individual characteristics (e.g., group, test experience, sex or age) to be more important than variables capturing transient experience (e.g., life events, testing arrangements or sociality). The study provides a solid foundation for the comparative study of great ape cognition.

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Introduction

In their quest to understand the evolution of cognition, anthropologists, psychologists, and cognitive scientists face one major obstacle: cognition does not fossilize. Instead of directly studying the cognitive abilities of, e.g., extinct early hominins, we have to rely on backward inferences. We can study fossilized skulls and crania to approximate brain size and structure and use this information to infer cognitive abilities (Coqueugniot, Hublin, Veillon, Houët, & Jacob, 2004; Gunz et al., 2020). We can study the material culture left behind by now-extinct species and try to infer its cognitive complexity experimentally (Coolidge & Wynn, 2016; Currie & Killin, 2019; Haslam et al., 2017). Yet, the archaeological record is sparse and only goes back so far in time. Thus, the comparative method is one of the most fruitful approaches to investigating cognitive evolution. By studying extant species of primates, we can make backward inferences about the last common ancestor. If species A and B both show cognitive ability X, the last common ancestor of A and B most likely also had ability X (Burkart, Schubiger, & Schaik, 2017; MacLean et al., 2012; Martins & Martins, 1996; Shettleworth, 2009). To make inferences about the most recent events in primate cognitive evolution, we have to study and compare humans and non-human great apes. Such an approach has been highly productive and provides the empirical basis for numerous theories about human cognitive evolution (Dean, Kendal, Schapiro, Thierry, & Laland, 2012; Dunbar & Shultz, 2017; Heyes, 2018; Laland & Seed, 2021; Penn, Holyoak, & Povinelli, 2008; Tomasello, 2019).

Applying the comparative method requires a comprehensive understanding of great ape cognition. Three kinds of empirical evidence are needed to rest species comparisons of cognition on solid grounds. First, group-level results must be stable: Inferences about the cognitive abilities of great apes – as a group, species or clade – must remain the same across repeated studies. Second, measures of individual differences in cognitive abilities should be reliable: Inferences about the cognitive abilities of any one great ape must remain the same across repeated studies. This is a prerequisite for investigating the relations between different cognitive abilities to map out the internal structure of great ape cognition (Matzel & Sauce, 2017; Shaw & Schmelz, 2017; Thornton & Lukas, 2012; Völter, Tinklenberg, Call, & Seed, 2018). Finally, variables that describe individual characteristics or aspects of everyday experience must systematically predict inter- and intra-individual variation in cognitive performance (Damerius et al., 2017; Horn, Cimarelli, Boucherie, Šlipogor, & Bugnyar, 2022).

Recently, several concerns have been voiced, questioning whether the prototypical way of conducting comparative cognitive studies is suited to provide the empirical basis for studying cognitive evolution (Farrar & Ostojic, 2019; ManyPrimates, Altschul, Beran, Bohn, Caspar, et al., 2019; Schubiger, Fichtel, & Burkart, 2020; Stevens, 2017). Most of this criticism revolves around issues that result from small sample sizes and researchers' degrees of freedom in analyzing and reporting data. An often overlooked but crucial additional criticism is that most research assumes that the three requirements outlined above are met without testing them empirically. The work reported here directly addresses this problem.

There are, however, several notable exceptions that undertook great effort to provide a more comprehensive picture of one or more aspects of the nature and structure of great ape cognition (Beran & Hopkins, 2018; Hopkins, Russell, & Schaeffer, 2014; MacLean et al., 2014; Wobber, Herrmann, Hare, Wrangham, & Tomasello, 2014). Herrmann and colleagues (Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007) tested more than one hundred great apes (chimpanzees and orangutans) and human children in a range of tasks covering numerical, spatial, and social cognition. The results indicated pronounced group-level differences between great apes and humans in the social but not the spatial or numerical domain. Furthermore, relations between the tasks pointed to a different internal structure of cognition, with a distinct social cognition factor for humans but not great apes (Herrmann, Hernández-Lloreda, Call, Hare, & Tomasello, 2010). Völter and colleagues

-Völter et al. (2022) focused on the structure of executive functions. Based on a multi-trait multi-method approach, they developed a new test battery to assess memory updating, inhibition, and attention shifting in chimpanzees and human children. Overall, they found low correlations between tasks and thus no clear support for structures put forward by theoretical models built around adult human data.

Despite their seminal contributions to the field, these studies suffer from one or more of the three shortcomings outlined above. It is unclear if the results are stable. If the same individuals were tested again, would the results license the same conclusions about absolute differences between species? Furthermore, the psychometric properties of the tasks are unknown and it is thus unclear if, for example, low correlations between tasks reflect a genuine lack of shared cognitive processes or simply measurement imprecision. Finally, which characteristics and experiences predict cognitive performance and development remains unclear.

The studies reported below seek to solidify the empirical grounds for investigating great ape cognition. For one-and-a-half years, every two weeks, we administered a set of five cognitive tasks (see Figure 1) to the same population of great apes ($N = 43$). The tasks spanned across cognitive domains and were based on published procedures widely used in comparative psychology. As a test of social cognition, we included a gaze following task (Bräuer, Call, & Tomasello, 2005). To assess causal reasoning abilities, we had a direct causal inference and an inference by exclusion task (Call, 2004). Numerical cognition was tested using a quantity discrimination task (Hanus & Call, 2007). Finally, as a test of executive functions, we included a delay of gratification task (Rosati, Stevens, Hare, & Hauser, 2007).

In addition to the cognitive data, we continuously collected 14 variables that capture stable and variable aspects of our participants' and their lives and used this to predict inter- and intra-individual variation in cognitive performance. Data collection was split into two phases. After Phase 1 (14 data collection time points), we analysed the data and registered the results (https://osf.io/7qyd8). Phase 2 lasted for another 14 time points and served to replicate and extend Phase 1. This approach allowed us to test a) how stable group-level results are, b) how stable individual differences are, c) how individual differences are structured and d) what predicts cognitive performance.

Results

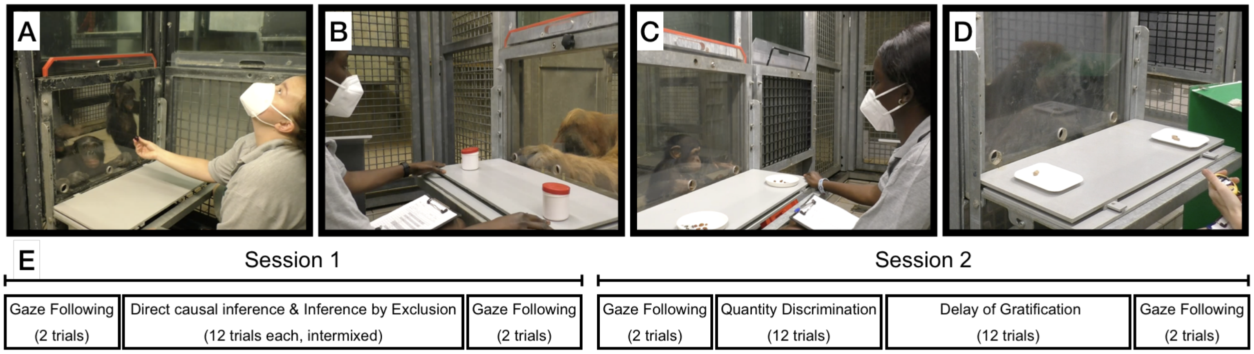
A
B
C
D
E
Session 1
Session 2
Gaze Following (2 trials)
Direct causal inference & Inference by Exclusion (12 trials each, intermixed)
Gaze Following (2 trials)
Gaze Following (2 trials)
Quantity Discrimination (12 trials)
Delay of Gratification (12 trials)
Gaze Following (2 trials)

Figure 1. Setup used for the five tasks. A) Gaze following: the experimenter looked to the ceiling. We coded if the ape followed gaze. B) Direct causal inference: food was hidden in one of two cups, the baited cup was shaken (food produced a sound) and apes had to choose the shaken cup to get food. Inference by exclusion: food was hidden in one of two cups. The empty cup was shaken (no sound), so apes had to choose the non-shaken cup to get food. C) Quantity discrimination: Small pieces of food were presented on two plates (5 vs. 7 items); we coded if subjects chose the larger amount. D) Delay of gratification (only Phase 2): to receive a larger reward, the subject had to wait and forgo a smaller, immediately accessible reward. E) Order of task presentation and trial numbers.

Stability of group-level performance

Group-level performance was largely stable or followed clear temporal patterns (see Figure 2). The direct causal inference and quantity discrimination tasks were the most robust: in both cases, performance was different from chance across both phases with no apparent change over time. The rate of gaze following declined at the beginning of Phase 1 but then settled on a low but stable level until the end of Phase 2. This pattern was expected given that following the experimenter's gaze was never rewarded – neither explicitly with food nor by bringing something interesting to the participant's attention. The inference by exclusion task showed an inverse pattern with group-level performance being at chance-level for most of Phase 1, followed by a small but steady increase throughout Phase 2. These temporal patterns most likely reflect training (or habituation) effects that are a *consequence* of repeated testing. Performance in the delay of gratification task (Phase 2 only) was more variable but within the same general range for the whole testing period. In sum, performance was very robust in that time points generally licensed the same group-level conclusions. The tasks appeared well suited to study group-level performance. In the supplementary material, we report additional analyses – Structural Equation Models (SEM) – that corroborate this interpretation.

Reliability of individual differences

Stable group-level performance does not imply stable individual differences. In fact, a well-known paradox in human cognitive psychology states that some of the most robust – on a group level – cognitive tasks do not produce stable individual differences (Hedge, Powell, & Sumner, 2018). In a second step, we, therefore, assessed the re-test correlations of our five tasks. For that, we correlated the performance at the different time points in each task. Figure 3 visualizes these re-test correlations. Correlations were generally high – some even exceptionally high for animal cognition standards (Cauchoix et al., 2018). As expected, values were also higher for more proximate time points (Uher, 2011). The quantity discrimination task had lower correlations compared to the other tasks. Based on re-test correlations alone, we cannot say whether lower correlations reflect higher measurement error (low reliability) or higher variability of individual differences across time (low stability). We

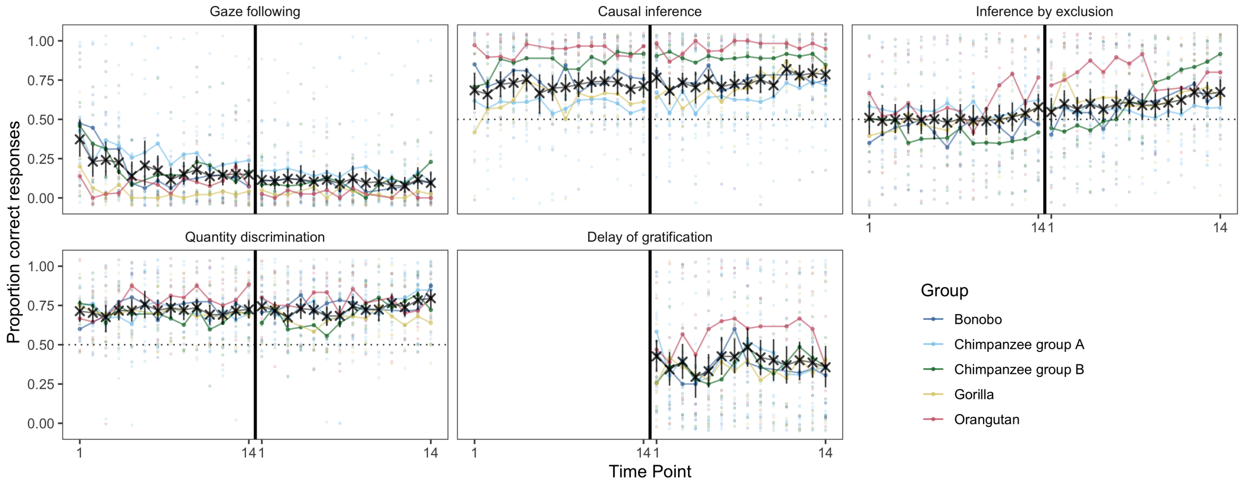

Figure 2. Results from the five cognitive tasks across time points. Black crosses show mean performance at each time point across species (with 95% CI). Colored dots show mean performance by species. Light dots show individual means per time point. Dashed lines show chance level whenever applicable. The vertical black line marks the transition between phases 1 and 2.

will tease these two components apart using SEM in the next section on the structure of individual differences.

As a final note, it stands out that *group-level stability does not imply individual-level stability* - and vice versa. The quantity discrimination task showed robust group-level performance above chance but relatively poor re-test correlations. In other words, even though group-level performance was stable, the ranking of individuals varied across time. In contrast, group-level performance in the inference by exclusion and gaze following tasks changed over time, but the ranking of individuals was relatively stable on an individual level. Nevertheless, we found that the majority of tasks were well suited for studying individual differences.

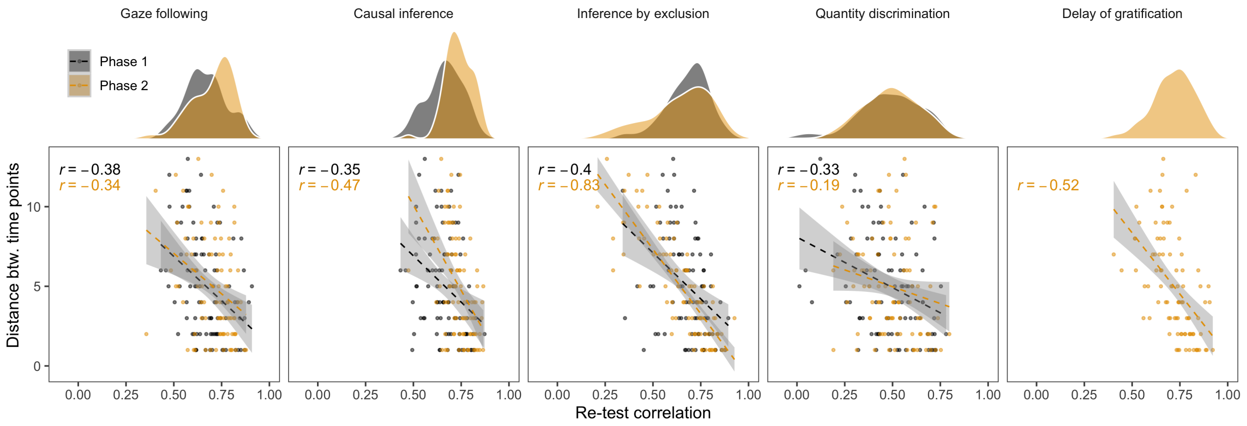

Figure 3. Top: Distribution of re-test Pearson correlation coefficients between time points for each task. Bottom: Pearson correlations between re-test correlation coefficients and temporal distance between the testing time points.

Structure of individual differences

Next, we investigated the structure of these individual differences. First, we asked to what extent individual differences reflect stable differences in cognitive abilities. We used structural equation modeling – in particular latent state-trait models (LSTM) – to partition the variance in performance into latent traits (*Consistency*), latent state residuals (*Occasion specificity*), and measurement error (Geiser, 2020; Steyer, Ferring, & Schmitt, 1992; Steyer, Mayer, Geiser, & Cole, 2015). In the present context, one can think of a latent trait as a stable cognitive ability (e.g., the ability to make causal inferences) and latent state residuals as variables capturing the effect of occasion-specific, variable psychological conditions (e.g., being more or less attentive or motivated). These latent variables are measurement-error-free because they are estimated by taking into account the reliability of the task. In the LSTM context, reliability is estimated as split-half reliability based on repeated parallel measurements per time point. We report additional models that account for the temporal structure of the data in the supplementary material.

Individual differences were largely explained by stable differences in cognitive abilities.

Across tasks, more than 75% of the reliable variance (true inter-individual differences) was accounted for by latent *trait* differences and less than 25% by *occasion-specific* variation between individuals (Figure 4A). The high reliability estimates ($>$ .75 for most tasks; see Figure 4A) show that these latent variables accounted for most of the variance in raw test scores – with the quantity discrimination task being an exception (reliability = .47). Reflecting back on the re-test correlations reported above, we can now say that these reflect measurement error rather than variable individual differences. In fact, consistency estimates for the quantity discrimination task were close to 1, reflecting highly stable true differences between individuals.

Next, we compared the estimates for the two phases of data collection. We found estimates for consistency and occasion specificity to be remarkably similar for the two phases. For inference by exclusion, we could not fit an LST model to the data from Phase 2 (see supplementary material for details). Instead, we divided Phase 2 into two parts (time points 1-8 and 9-14) and estimated a separate trait for each part. All estimates were similar for both parts (Figure 4A), and the two traits were highly correlated ($r = .82$). Together with additional latent state models, which we report in the supplementary material, this suggests that the increase in group-level performance in Phase 2 was driven by a relatively sudden improvement of a few individuals, mostly from the chimpanzee B group (see Figure 2). These individuals "rose through the ranks" halfway through Phase 2 and then retained this position for the rest of the study. Some of the orangutans changed in the opposite direction – though to a lesser extent.

Finally, we investigated the relations between latent traits. That is, we asked whether individuals with high abilities in one domain also have higher abilities in another. We fit pairwise LST models that modeled the correlation between latent traits for two tasks (two models for inference by exclusion in Phase 2). In Phase 1, the only correlation that was reliably different from zero was between quantity discrimination and inference by exclusion. In Phase 2, this finding was replicated, and, in addition, four more correlations turned out to be substantial (see Figure 4B). One reason for this increase was the inclusion of the delay of gratification task. Across phases, correlations involving the gaze following task were the closest to zero, with quantity discrimination in Phase 2 being an exception. Taken together, the overall pattern of results suggests substantial shared variance between tasks – except for gaze following.

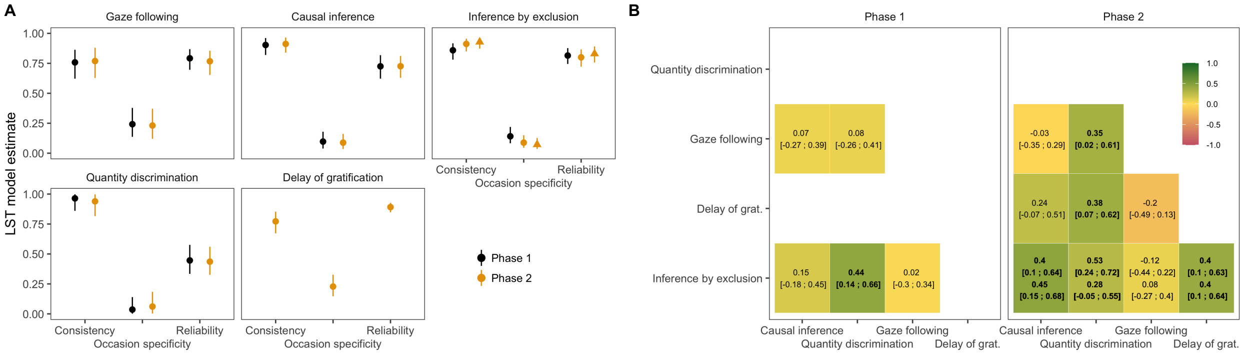

Figure 4. A. Estimates from latent state-trait models for Phase 1 and 2. Consistency: proportion of (measurement-error-free) variance in performance explained by stable trait differences. Occasion specificity: true variance explained by variable state residuals. Reliability: proportion of variance in raw scores explained by the trait and the state residual variables. For inference by exclusion: different shapes show estimates for different parts of Phase 2 (see main text for details). B. Correlations between latent traits based on pairwise LST models between tasks with 95% Credible Interval. Bold correlations are reliably different from zero. Inference by exclusion has one value per part in Phase 2. The models for quantity discrimination and direct causal inference showed a poor fit and are not reported here (see supplementary material for details).

Predictability of individual differences

The results thus far suggest that individual differences originate from stable differences in cognitive abilities. In the last set of analyses, we sought to explain the origins of these differences. That is, we analysed whether inter- and intra-individual variation in cognitive performance in the tasks could be predicted by non-cognitive variables that captured a) stable differences between individuals (group, age, sex, rearing history, time spent in research), b) differences that varied within and between individuals (rank, sickness, sociality), c) differences that varied with group membership (time spent outdoors, disturbances, life events), and d) differences in testing arrangements (presence of observers, study participation on the same day and since the last time point). We collected these predictor variables using a combination of directed observations and caretaker questionnaires.

This large set of potentially relevant predictors poses a variable selection problem. Thus, in our analysis, we sought to find the minimal set of predictors that allowed us to accurately predict performance in the cognitive tasks. We chose the projection predictive inference approach because it provides an excellent trade-off between model complexity and accuracy (Pavone, Piironen, Bürkner, & Vehtari, 2020; Piironen, Paasiniemi, & Vehtari, 2020; Piironen & Vehtari, 2017). The outcome of this analysis is a ranking of the different predictors in terms of how important they are to predict performance in a given task. Furthermore, for each predictor, we get a qualitative assessment of whether it makes a substantial contribution to predicting performance in the task or not.

Predictors capturing stable individual characteristics were ranked highest and selected as relevant most often (Figure 5). The four highest-ranked predictors belonged to this category. This result aligned well with the LSTM results reported above, in which we saw that most of the variance in performance could be traced back to stable trait differences between individuals. The tasks with the highest occasion-specific variance (gaze following and delay of gratification, see Figure 4) were also those for which the most time point specific predictors were selected. The quantity discrimination task did not fit this pattern in Phase 2; even though the LSTM suggested that only a very small portion of the variance in performance was occasion-specific, four time-point-specific variables were selected to be relevant.

The most important predictor was group. Interestingly, differences between groups were not systematic in that one group would consistently outperform the others across tasks. Furthermore, group differences could not be collapsed into species differences as the two chimpanzee groups varied largely independent of one another (Figure 5B). Predictors that were selected more than once influenced performance in variable ways. The presence of observers always had a negative effect on performance. The more time an individual had been involved in research during their lifetime, the better performance was. Higher-ranking individuals outperformed lower-ranking ones. On the other hand, while the rate of gaze following increased with age, performance in the inference by exclusion task decreased. Females were more likely to follow gaze than males, but males were more likely to wait for the larger reward in the delay of gratification task. Time spent outdoors had a positive effect on gaze following but a negative effect on direct causal inference. Finally, individuals with stronger reported health problems were less likely to follow gaze but more likely to delay gratification (Figure 5B).

In sum, of the predictors we recorded, those capturing stable individual characteristics were most predictive of cognitive performance. In most cases, these predictors were also selected as relevant in both phases. The influence of time-point-specific predictors was less consistent: except for the presence of an observer in the gaze following task, none of the variable predictors was selected as relevant in both phases. To avoid misinterpretation, this suggests that cognitive performance *was* influenced by temporal variation in group life, testing arrangements and variable characteristics; however, the way this influence exerts itself was either less consistent or less pronounced (or both).

It is important to note, however, that in terms of absolute variance explained, the largest portion was accounted for by a random intercept term in the model (not shown in Figure 5) that simply captured the identity of the individual (see supplementary material for details). This suggests that idiosyncratic developmental processes or genetic pre-dispositions, which operate on a much longer time scale than what we captured in the present study, were responsible for most of the variation in cognitive performance.

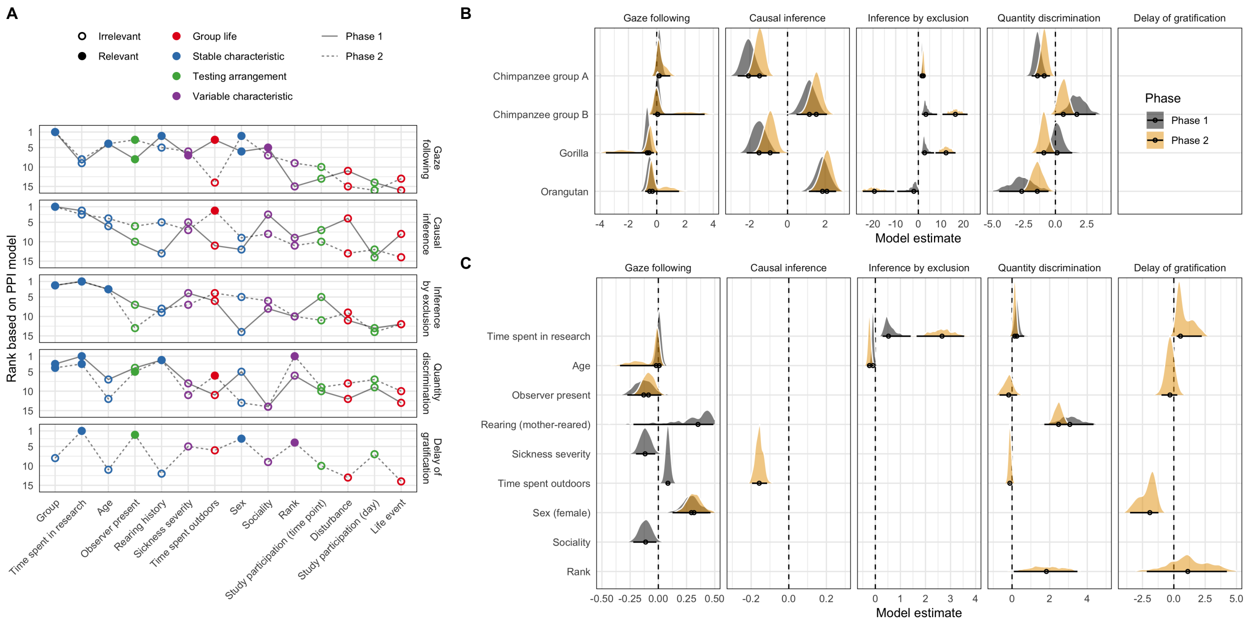

Figure 5. A. Ranking of predictors based on the projection predictive inference model for the five tasks in the two phases. Order (left to right) is based on average rank across phases. Solid points indicate predictors selected as relevant. Color of the points shows the category of the predictor. Line type denotes the phase. B. Posterior model estimates for the selected predictors for each task. Crosses show the mean of the posterior distribution and error bars the 95% Credible Interval. Color denotes phase. Black rectangles zoom in on the predictors that are numerically too small to show whether they have a positive or negative influence on performance.

Discussion

The goal of this study was to test the assumptions underlying much of comparative research and theorizing about cognitive evolution. We repeatedly tested a large sample of great apes in five tasks covering a range of different cognitive domains. We found group-level performance to be relatively stable so that conclusions drawn based on one testing occasion mirrored those on other occasions. Most of the tasks measured differences between individuals in a reliable and stable way – making them suitable to study individual differences. Using structural equation models, we found that individual differences in performance were largely explained by traits – that is, stable differences in cognitive abilities between individuals. Furthermore, we found systematic relations between cognitive abilities. When predicting variation in cognitive performance, we found stable individual characteristics (e.g., group or time spent in research) to be the most important. Variable predictors were also found to be influential at times but in a less systematic way.

At first glance, the results send a reassuring message to the field: most of the tasks that we used produced stable group-level results and captured individual differences in a reliable and stable way. However, this did not apply to all tasks. In the supplementary material, we report on a rule-switching task (Haun, Call, Janzen, & Levinson, 2006) that produced neither stable nor reliable results. The quantity discrimination task was stable on a group level but less reliable on an individual level. We draw two conclusions based on this pattern. First, replicating studies – even if it is with the same animals – should be an integral part of primate cognition research (Farrar, Boeckle, & Clayton, 2020; ManyPrimates, Altschul, Beran, Bohn, Caspar, et al., 2019; Stevens, 2017). Second, for individual differences research, it is crucial to assess the psychometric properties (reliability, stability) of the measures involved (Fried & Flake, 2018). If this step is omitted, it is difficult to interpret studies, especially when they produce null-results. It is important to note that the sample size in the current study was large compared to other comparative studies (median sample size = 7, see ManyPrimates, Altschul, Beran, Bohn, Caspar, et al., 2019). With smaller sample sizes, group-level and reliability estimates are more likely to be more variable and thus more likely to produce false-positive or false-negative conclusions (Forstmeier, Wagenmakers, & Parker, 2017; Oakes, 2017). Small samples in comparative research usually reflect resource limitations of individual labs. Pooling resources in large-scale collaborative projects like *ManyPrimates* (ManyPrimates et al., 2021; ManyPrimates, Altschul, Beran, Bohn, Call, et al., 2019) will thus be vital to corroborate findings. Some research questions –

for example, the distinction between group- vs. species-level explanations of primate cognitive performance (Van Leeuwen, Cronin, & Haun, 2018) – cannot even be addressed with a single population of primates.

Given their good psychometric properties, our tasks offer insights into the structure of great ape cognition. We used structural equation modeling to partition reliable variance in performance into stable (trait) and variable (state) differences between individuals. We found traits to explain more than 75% of the reliable variance across tasks. This suggests that stable differences in cognitive abilities and not variable differences in, e.g., attention and motivation are responsible for the patterns we observed. This finding does not mean that there is no developmental change over time. In fact, for the inference by exclusion task, we saw a relatively abrupt change in performance for some individuals, which stabilized on an elevated level, suggesting sustained change in cognitive abilities. With respect to structure, we found systematic relations between traits estimated via LSTMs for the different tasks. Correlations tended to be higher among the non-social tasks compared to when the gaze following task was involved, which could be taken to hint at shared cognitive processes. However, we feel such a conclusion would be premature and would require additional evidence from more tasks and larger sample sizes (Herrmann et al., 2010). Furthermore, cognitive modeling could be used to explicate the processes involved in each task. Shared processes could be probed by comparing models that make different assumptions about overlapping processes (Bohn, Liebal, & Tessler, 2022; Devaine et al., 2017). For example, a model in which direct causal inference is a sub-process of inference by exclusion could be compared to a model assuming distinct reasoning processes for the two tasks.

The finding that stable differences in cognitive abilities explained most of the variation between individuals was also corroborated by the analyses focused on the predictability of performance. We found that predictors that captured stable individual characteristics (e.g., group, time spent in research, age, rearing history) were more likely to improve model fit. Aspects of everyday experience or testing arrangements that would influence performance on particular time points and thus increase the proportion of occasion-specific variation (e.g., life events, disturbances, participating in other tests) were ranked as less important. Despite this general pattern, there was, however, variation across tasks in which individual characteristics were selected to be relevant. For example, rearing history turned out to be an important predictor for quantity discrimination and gaze following but less so for the other three tasks (Figure 5A). Group – the overall most important predictor – exerted its influence differently across tasks. Orangutans, for example, outperformed the other groups in direct causal inference but were the least likely to follow gaze. Together with the finding that the random intercept term improved model fit the most across tasks, this pattern suggests that the cognitive abilities underlying performance in the different tasks respond to different – though sometimes overlapping – external conditions that together shape the individual's developmental environment.

Our results also address a very general issue. Comparative psychologists often worry – or are told they should worry – that their results can be explained by mechanistically simpler associative learning processes (Hanus, 2016). Oftentimes such explanations are theoretically plausible and hard to disprove empirically. The present study speaks to this issue in so far as we created optimal conditions for such associative learning processes to unfold. Great apes were tested by the same experimenter in the same tasks, using differential reinforcement and the same counterbalancing for hundreds of trials. The steady increase in performance – uniform over individuals – that an associative learning account would predict did not show. Instead, when we saw change over time, performance either decreased (gaze following) or increased at a late point in time for only a few individuals (inference by exclusion). This does not take away the theoretical possibility that associative learning accounts for improved performance over time on isolated tasks; it just makes them less useful given that their predictions do not bear out as a general pattern.

Conclusion

The present study put the implicit assumptions underlying much of comparative research on cognitive evolution involving great apes to an empirical test. While we found reassuring results in terms of group-level stability and reliability of individual differences, we also pointed out the importance of explicitly questioning and testing these assumptions, ideally in large-scale collaborative projects. Our results paint a picture of great ape cognition in which variation between individuals is predicted and explained by stable individual characteristics that respond to different – though sometimes overlapping – developmental conditions. Hence, an ontogenetic perspective is not auxiliary, but fundamental to studying cognitive diversity across species. We hope these results contribute to a more solid and comprehensive understanding of the nature and origins of great ape and human cognition as well as provide useful methodological guidance for future comparative research.

Methods

A detailed description of the methods and results can be found in the supplementary material available online. All data and analysis scripts can be found in the associated online repository (https://github.com/ccp-eva/laac).

Participants

A total of 43 great apes participated at least once in one of the tasks. This included 8 Bonobos (3 females, age 7.30 to 39), 24 Chimpanzees (18 females, age 2.60 to 55.90), 6 Gorillas (4 females, age 2.70 to 22.60), and 5 Orangutans (4 females, age 17 to 41.20). The overall sample size at the different time points ranged from 22 to 43 for the different species.

Apes were housed at the Wolfgang Köhler Primate Research Center located in Zoo Leipzig, Germany. They lived in groups, with one group per species and two chimpanzee groups (groups A and B). Studies were noninvasive and strictly adhered to the legal requirements in Germany. Animal husbandry and research complied with the European Association of Zoos and Aquaria Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria as well as the World Association of Zoos and Aquariums Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquariums. Participation was voluntary, all food was given in addition to the daily diet, and water was available ad libitum throughout the study. The study was approved by an internal ethics committee at the Max Planck Institute for Evolutionary Anthropology.

Material

Apes were tested in familiar sleeping or test rooms by a single experimenter. Whenever possible, they were tested individually. The basic setup comprised a sliding table positioned in front of a clear Plexiglas panel with three holes in it. The experimenter sat on a small stool and used an occluder to cover the sliding table (see Figure 1).

Procedure

The tasks we selected are based on published procedures and are commonly used in the field of comparative psychology. Example videos for each task can be found in the associated online repository.

Gaze Following. The gaze following task was modeled after Bräuer et al. (2005). The experimenter sat opposite the ape and handed over food at a constant pace. That is, the experimenter picked up a piece of food, briefly held it out in front of her face and then handed it over to the participant. After a predetermined (but varying) number of food items had been handed over, the experimenter again picked up a food item, held it in front of her face and then looked up (i.e., moving her head up - see Figure 1A). The experimenter looked to the ceiling; no object of particular interest was placed there. After 10s, the experimenter looked down again, handed over the food and the trial ended. We coded whether the participant looked up during the 10s interval. Apes received eight gaze-following trials. We assume that participants look up because they assume that the experimenter's attention is focused on a potentially noteworthy object.

Direct causal inference. The direct causal inference task was modeled after Call (2004). Two identical cups with a lid were placed left and right on the table (Figure 1B). The experimenter covered the table with the occluder, retrieved a piece of food, showed it to the ape, and hid it in one of the cups outside the participant's view. Next, the experimenter removed the occluder, picked up the baited cup and shook it three times, which produced a rattling sound. Next, the cup was put back in place, the sliding table pushed forwards, and the participant made a choice by pointing to one of the cups. If they picked the baited cup, their choice was coded as correct, and they received the reward. If they chose the empty cup, they did not. Participants received 12 trials. The location of the food was counterbalanced; six times in the right cup and six times in the left. Direct causal inference trials were intermixed with inference by exclusion trials (see below). We assume that apes locate the food by reasoning that the food – a solid object – causes the rattling sound and, therefore, must be in the shaken cup.

Inference by exclusion. Inference by exclusion trials were also modeled after Call (2004) and followed a very similar procedure compared to direct causal inference trials. After covering the two cups with the occluder, the experimenter placed the food in one of the cups and covered both with the lid. Next, they removed the occluder, picked up the empty cup and shook it three times. In contrast to the direct causal inference trials, this did not produce any sound. The experimenter then pushed the sliding table forward and the participant made a choice by pointing to one of the cups. Correct choice was coded when the baited (non-shaken) cup was chosen. If correct, the food was given to the ape. There were 12 inference by exclusion trials intermixed with direct causal inference trials. The order was counterbalanced: six times the left cup was baited, six times the right. We assume that apes reason that the absence of a sound suggests that the shaken cup is empty. Because they saw a piece of food being hidden, they exclude the empty cup and infer that the food is more likely to be in the non-shaken cup.

Quantity discrimination. For this task, we followed the general procedure of Hanus and Call (2007). Two small plates were presented left and right on the table (see Figure 1C). The experimenter covered the plates with the occluder and placed five small food pieces on one plate and seven on the other. Then they pushed the sliding table forwards, and the participant made a choice. We coded as correct when the subject chose the plate with the larger quantity. Participants always received the food from the plate they chose. There were 12 trials, six with the larger quantity on the right and six on the left (order counterbalanced). We assume that apes identify the larger of the two food amounts based on discrete quantity estimation.

Delay of gratification. This task replaced the switching task in Phase 2. The procedure was adapted from Rosati et al. (2007). Two small plates, including one and two pieces of pellet, were presented left and right on the table. The experimenter moved the plate with the smaller reward forward, allowing the subject to choose immediately, while the plate with the larger reward was moved forward after a delay of 20 seconds. We coded whether the subject selected the larger delayed reward (correct choice) or, the smaller immediate reward (incorrect choice) as well as the waiting time in cases where the immediate reward was chosen. Subjects received 12 trials, with the side on which the immediate reward was presented counterbalanced. We assume that, in order to choose the larger reward, apes inhibit choosing the immediate smaller reward.

Data collection

We collected data in two phases. Phase 1 started on August 1st, 2020, lasted until March 5th, 2021, and included 14 time points. Phase 2 started on May 26th, 2021 and lasted until December 4th, 2021 and also had 14 time points. Phase 1 also included a strategy switching task. However, because it did not produce meaningful results, we replaced it with the delay of gratification task. Details and results can be found in the supplementary material available online.

One time point meant running all tasks with all participants. Within each time point, the tasks were organized in two sessions (see Figure 1E). Session 1 started with two gaze following trials. Next was a pseudo-randomized mix of direct causal inference and inference by exclusion trials with 12 trials per task but no more than two trials of the same task in a row. At the end of Session 1, there were again two gaze following trials. Session 2 also started with two gaze following trials, followed by quantity discrimination and strategy switching (Phase 1) or delay of gratification (Phase 2). Finally, there were again two gaze following trials. The order of tasks was the same for all subjects. So was the positioning of food items within each task. The two sessions were usually spread out across two adjacent days. The interval between two time points was planned to be two weeks. However, it was not always possible to follow this schedule, so some intervals were longer or shorter. Figure S1 in the supplementary material shows the timing and spacing of the time points.

In addition to the data from the cognitive tasks, we collected data for a range of predictor variables. Predictors could either vary with the individual (stable individual characteristics: group, age, sex, rearing history, time spent in research), vary with individual and time point (variable individual characteristics: rank, sickness, sociality), vary with group membership (group life: e.g., time spent outdoors, disturbances, life events) or vary with the testing arrangements and thus with individual, time point and session (testing arrangements: presence of observers, study participation on the same day and since the last time point). Most predictors were collected via a diary that the animal caretakers filled out on a daily basis. Here, the caretakers were asked a range of questions about the presence of a predictor and its severity. Other predictors were based on direct observations. A detailed description of the predictors and how they were collected can be found in the supplementary material available online.

Analysis

In the following, we provide an overview of the analytical procedures we used. We encourage the reader to consult the supplementary material available online for additional details and results.

We had two overarching questions. On the one hand, we were interested in the cognitive measures and the relations between them. That is, we asked how stable performance in a given task was on a group-level, how stable individual differences were, and how reliable the measures were. We also investigated relations between the different tasks. We used *Structural Equation Modeling* (SEM) (Bollen, 1989; Hoyle, 2012) to address these questions.

Our second question was, which predictors explain variability in cognitive performance. Here we wanted to see which of the predictors we recorded were most important to predict performance over time. This is a variable selection problem (selecting a subset of variables from a larger pool) and we used *Projection Predictive Inference* for this (Piironen et al., 2020).

Structural equation modeling.

We used Structural Equation Modeling (SEM) (Bollen, 1989; Hoyle, 2012) to address the stability and structure of each task, as well as relations between tasks. SEMs allowed us to partition the variance in performance into latent traits (stable over time), latent state residuals (time varying deviations from the stable trait), and measurement error. Because the latent variables are estimated on multiple indicators (here: test halves), they are assumed to be measurement-error-free (Geiser, 2020; Steyer et al., 1992, 2015). In the present context, one can think of a trait as a stable psychological ability (e.g., ability to make causal inferences) and state residuals as time-specific deviations from these traits due to variable psychological conditions (e.g., variations in performance due to being attentive or inattentive).

We used Bayesian estimation techniques to estimate the models. In the supplementary material available online, we report the prior settings used for estimation as well as the structural restrictions we imposed on the model parameters. We justify these settings and restrictions via simulation studies also included in the supplementary material.

In our focal Latent Trait-State (LST) model, the observed categorical variables Y_{it} for test half i at time point t result from a categorization of unobserved continuous latent variables Y^*_{it} which underlie the observed categorical variables (graded response model, see Samejima, 1969, 1996). This continuous latent variable Y^*_{it} is then decomposed into a latent trait variable T_{it}, a latent state residual variable ζ_{it}, and a measurement error variable. The latent trait variables T_{it} are time-specific dispositions, that is, trait scores that capture the expected value of the latent state (i.e., true score) variable for an individual at time t across all possible situations the individual might experience at time t (Eid, Holtmann, Santangelo, & Ebner-Priemer, 2017; Steyer et al., 2015). The state residual variables ζ_{it} capture the deviation of a momentary state from the time-specific disposition T_{it}. We assumed that latent traits were stable across time. In addition, we assumed common latent trait and state residual variables across the two test halves, which leads to the following measurement equation for parcel i at time point t:

$$Y^*_{it} = T + \zeta_t + \epsilon_{it} \tag{1}$$

Here, T is a stable (time-invariant) latent trait variable, capturing stable inter-individual differences. The state residual variable ζ_t captures time-specific deviations of the respective true score from the trait variable at time t, and thereby captures deviations from the trait due to situation or person-situation interaction effects. ϵ_{it} denotes a measurement error variable, with $\epsilon_{it} \sim N(0,1)\ \forall\ i,t$. This allowed us to compute the following variance components.

Consistency: Proportion of true variance (i.e., measurement-error free variance) that is due to true inter-individual stable trait differences.

$$Con(Y_{it}^{*}) = \frac{Var(T)}{Var(T) + Var(\zeta_t)} \tag{2}$$

Occasion specificity: Proportion of true variance (i.e., measurement-error free variance) that is due to true inter-individual differences in the state residual variables (i.e., occasion-specific variation not explained by the trait).

$$OS(Y_{it}^{*}) = 1 - Con(Y_{it}^{*}) = \frac{Var(\zeta_t)}{Var(T) + Var(\zeta_t)} \tag{3}$$

As state residual variances $Var(\zeta_t)$ were set equal across time, $OS(Y_{it}^{*})$ is constant across time (as well as across item parcels i).

To investigate associations between cognitive performance in different tasks, the LSTMs were extended to multi-trait models. Due to the small sample size, we could not combine all tasks in a single, structured model. Instead, we assessed relations between tasks in pairs.

Projection predictive inference. The selection of relevant predictor variables constitutes a variable selection problem, for which a range of different methods are available (e.g., shrinkage priors, Van Erp, Oberski, & Mulder, 2019). We chose to use *Projection Predictive Inference* because it provides an excellent trade-off between model complexity and accuracy (Piironen et al., 2020; Piironen & Vehtari, 2017), especially when the goal is to identify a minimal subset of predictors that yield a good predictive model (Pavone et al., 2020).

The projection predictive inference approach can be viewed as a two-step process: The first step consists of building the best predictive model possible, called the reference model. In the context of this work, the reference model is a Bayesian multilevel regression model (repeated measurements nested in apes, fit using the package `brms`, Bürkner, 2017), including all 14 predictors and a random intercept term for the individual (`R` notation: `DV ~ predictors + (1 | subject)`).

In the second step, the goal is to replace the posterior distribution of the reference model with a simpler distribution. This is achieved via a forward step-wise addition of predictors that decrease the Kullback-Leibler (KL) divergence from the reference model to the projected model.

The result of the projection is a list containing the best model for each number of predictors from which the final model is selected by inspecting the mean log-predictive density (elpd) and root-mean-squared error (rmse). The projected model with the smallest number of predictors is chosen, which shows similar predictive performance as the reference model.

We built separate reference models for each phase and task and ran them through the above-described projection predictive inference approach. The dependent variable for each task was the cognitive performance of the apes, that is, the number of correctly solved trials per time point and task. The model for the delay of gratification task was only estimated once (Phase 2).

Following step two, we performed projection predictive inference for each reference model separately, thus resulting in different rankings for the relevant predictors for each task and phase. We used the R package projpred (Piironen, Paasiniemi, Catalina, Weber, & Vehtari, 2022), which implements the aforementioned projection predictive inference technique. The predictor relevance ranking is measured by the Leave-One-Out (LOO) cross-validated mean log-predictive density and root-mean-squared error. To find the optimal submodel size, we inspected summaries and the plotted trajectories of the calculated elpd and rmse.

The order of relevance for the predictors and the random intercept (together called terms) is created by performing forward search. The term that decreases the KL divergence between the reference model's predictions and the projection's predictions the most goes into the ranking first. Forward search is then repeated N times to get a more robust selection.

We chose the final model by inspecting the predictive utility of each projection. To be precise, we chose the model with p terms where p depicts the number of terms at the cutoff between the term that increases the `elpd` and the term that does not increase the `elpd` by any significant amount. In order to get a useful predictor ranking, we manually delayed the random intercept (and random slope for time point for gaze following) term to the last position in the predictor selection process. The random intercept delay is needed because if the random intercept were not delayed, it would soak up almost all of the variance of the dependent variable before the predictors are allowed to explain some amount of the variance themselves.

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Competing interest

The authors declare that no competing interests exist.