

Title: The evolution of transitive inference: Chimpanzees' performance with social and nonsocial stimuli

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Abstract

A number of theories posit various social and nonsocial factors as the central drivers of the evolution of intelligence. Cognitive skills, such as transitive interference, that have important implications in both the social and nonsocial domains can help identify drivers of cognitive evolution. Transitive inference is an inferential reasoning skill, which allows individuals to deduce unknown relationships from known ones. Due to its importance in both social and nonsocial contexts it can provide a powerful test of the driving forces behind primate cognitive evolution. We compared chimpanzees' (*Pan troglodytes*) performance on social and nonsocial versions of a transitive inference task in order to assess whether they are better adapted to apply transitive reasoning to social or nonsocial stimuli. Our preliminary findings provide partial support for the hypotheses that chimpanzees are better adapted to use transitive inference in the social and nonsocial domains. However, our statistical abilities are limited by a small sample size and several confounding factors regarding the age and sex of our subjects, which limit firm conclusions. Further research (outlined in our methods) will allow us to more accurately assess the factors associated with the evolution of transitive inference skills in chimpanzees.

Introduction

One of the greatest challenges facing evolutionary anthropologists today is determining the driving force behind the evolution of intelligence. Much of the debate so far has centered on the importance of social versus nonsocial factors. The evolutionary correlates of certain behaviors are especially difficult to determine for

aspects of general intelligence, which clearly have important implications for both the social and nonsocial domain. Tinbergen (1963) argued that before a behavior could be fully understood four central questions had to be answered. These questions concerned the behavior's proximate causes – mechanism and ontogeny -- and its ultimate causes – function and phylogeny. Although progress has been made in addressing these questions for certain adapted behaviors, determining the evolutionary causes of others remains challenging. Throughout the literature there is no consensus as to the relative importance of social factors such as group size versus nonsocial factors such as diet in driving cognitive evolution (Holekamp 2006; MacLean *et al.* 2008). The present study seeks to inform this debate by examining the role of group living and other selective pressures in shaping inferential reasoning skills, specifically transitive inference, in chimpanzees (*Pan troglodytes*) by comparing their performance on a social and nonsocial version of a transitive inference task.

A number of hypotheses have been proposed to explain the evolution of cognition. These hypotheses fall largely into two categories, those that posit social factors and those that posit nonsocial factors as the primary driving force of cognitive evolution. The social hypotheses highlight the importance of social factors in the cognitive evolution of primates (Bryne & Whiten 1997). These center on the notion that primates evolved in response to complex problems associated with group living and that social intelligence preceded nonsocial intelligence (Bryne & Whiten 1997). Specifically, the social intelligence hypothesis states that primate cognition evolved primarily in response to the complex demands associated with

group living (Bryne & Whiten 1989). In contrast nonsocial hypotheses rest on the importance of either general intelligence or other factors such as ecology in allowing for the selection of intelligence (Milton 1981).

Nonsocial hypotheses

Ecological intelligence hypotheses suggest that foraging challenges drove the evolution of cognition. An individual's ability to remember locations and phenological distributions of resources are believed to be related to foraging success and therefore ultimately reproductive success (Erhart & Overdorff 2006). Milton (1981) hypothesized that finding spatially and temporally scattered food sources posed major cognitive challenges for memory and spatial representation and have therefore been a major force in the evolution of primate intelligence. In lemurs significant correlations between relative brain size and diet and activity pattern support Milton's conjecture (MacLean *et al.* 2009). There appear to be more challenges associated with frugivory compared with folivory as it requires individuals to remember the spatial locations of fruiting trees as well as the timing of fruiting and ripening. In contrast folivory is relatively simpler as leaves tend to be ubiquitous although Milton (1984) notes that plants do put forth both physical and chemical defenses in response to predation. Aeillo and Wheeler (1995) added additional caveats to this theory by putting forth the Expensive-Tissue hypothesis, which states that because brain tissue is metabolically costly increases in brain size have to be offset by either a reduction in gut size or a shift to a higher quality diet. Therefore they posit that regardless of what drove the evolution of primate cognition it would not have been possible without increasing diet quality.

Furthermore Holekamp (2006) points out what he believes are a number of inconsistencies and phenomena that aren't predicted by social intelligence hypotheses. For example throughout evolutionary time there is a covariation between increases in brain volume in ungulates and increases in brain volume in carnivores, which is expected based on the idea of an "evolutionary arms race". However these brain volume increases occurred both in social and nonsocial carnivores, which the social intelligence hypothesis doesn't predict (Holekamp 2006). Reader and Laland (2002) also found that social group size and social learning frequency were not correlated with each other indicating an absence of strong support for the social intelligence hypothesis. Instead they suggested that their data supported ecological hypotheses and the "technical intelligence" hypothesis, which posits that technical skills drove primate cognitive evolution. Their support for the technical intelligence hypothesis stems from their finding of a correlation between incidences of tool use and executive brain ratio (Reader & Laland 2002). These hypotheses also rest on the fact that a number of ecological factors such as diet are positively correlated with brain volume (Holekamp 2006). However a large and growing body of evidence continues to provide support for the social intelligence hypothesis.

Social hypotheses

Humphrey (1976) argued that cognitive abilities evolved in response to social complexities. He posited that when competing with conspecifics for access to mates selection will always favor individuals who can outcompete or outwit their competitors in essence creating and "evolutionary ratchet". In response to the many

traditional ecological hypotheses and in the line of support of Humphrey, Byrne and Whiten (1989) proposed the Machiavellian Intelligence Hypothesis. This hypothesis states that intelligence likely evolved as an adaptation to help individuals navigate the complex demands of living in a group such as cooperating or competing with conspecifics (Byrne & Whiten 1989). Since that time the theories emphasizing the social component of evolving intelligence have been expanded and are now commonly grouped under the social brain hypothesis (Dunbar & Schultz 2007). In support for the social brain hypothesis, many studies have shown that various measures of brain size correlate robustly with measures of group size across primates. For example larger brain size is correlated with frequency of social learning (Reader & Laland 2002), prevalence of social play (Lewis 2000), frequency of tactical deception (Byrne & Corp 2004), frequency of coalitions (Dunbar & Schultz 2007), grooming group size (Kudo & Dunbar 2001), number of females (Lindenfors 2005), and social group size (Dunbar 1992). Furthermore Silk *et al.* (1999) demonstrated a direct link between sociality and reproductive success by showing that more social females experienced greater reproductive success than less social females. Sociality has clearly played an important role in the evolution of primate cognition as it stands to reason that primates have evolved in response to increasing social complexities.

Adaptation or a byproduct of selection

Beyond the debate over whether increasing complexity in primate cognition arose as a result of ecological or social challenges there is also a debate over whether the specific aspects of cognition we study arose as their own adaptations or

as a byproduct of selection for other more general traits. For example in the infamous Siberian fox experiments researchers selectively bred foxes based on whether they fearlessly and non-aggressively approached a human. This trait in this artificial context could be considered the adaptation but unexpectedly these “friendlier” foxes also had higher incidences of floppy ears, depigmentation of hair, and short or curly tails among other things (Hare & Tomasello 2005). All of these additional factors were byproducts of selection for fearlessness and nonaggression. Although in this artificial context it is easy to separate the two this is less true in regard to already developed traits. This challenge can also be conceptualized in terms of domain specificity, which is the notion that adaptations evolve to solve problems in particular domains, and therefore are less well suited to solve problems in other domains. For example if a trait is domain general it is possible that social and nonsocial pressures selected for the trait's evolution, but if it's domain specific then it should be shaped by selective pressures associated with that domain. There is also a third possibility that it was originally domain specific but later co-opted. In this scenario it would be initially built for nonsocial purposes by nonsocial selective pressures and only later co-opted for social functions by social pressures. It can be challenging to discriminate between these varying scenarios. Chiappe and MacDonald (2010) argue that domain general mechanisms are an important component of cognition because they allow individuals to confront the fundamental problem of new challenges that arise as a result of continually changing and fluctuating environments.

Transitive inference

Understanding the relationship among various entities, whether they be social agents, tools or food, can be important for prioritizing actions and choices. Transitive inference is an inferential reasoning skill that can help individuals conceptualize the relationship among many elements by allowing them to compare previously unknown or disparate relationships. Creating a mental hierarchy allows individuals to understand the relationship between two previously uncomparing objects by knowing their relationship to a third object. For example, if in a linear hierarchy individual A is dominant to individual B and B is dominant to C then one can infer that A is also dominant to C. Transitive inference is an important cognitive skill because organizing information in a linear order is extremely efficient as it allows individuals to preserve all essential information and make deductions about novel relations within the series (Davis 1992). It was originally believed to be a skill that belonged exclusively to humans but has now been found in a wide range of species from fish to birds to nonhuman primates (White & Gowan, 2012; Mikolash *et al.*, 2013; MacLean *et al.* 2008). Since transitive inference has important implications in both social and nonsocial domains it could expose key information about cognitive evolution.

Nonsocial implications of transitive inference

Although there are fewer documented applications of transitive inference in the nonsocial domain it clearly could have important implications. Rosati and Hare (2012) conducted food preference tests where they allowed chimpanzees to create their own hierarchy of most to least preferred food items. Although there was no component of transitive inference this task demonstrated that chimpanzees can

organize food into linear hierarchies as well. Another study found that wild orangutans, *Pongo pygmaeus*, make foraging decisions based on a variety of factors including patch size, level of toxins, and energy content (Leighton 1993). It is possible that they are organizing this information hierarchically in order to make the best foraging decisions in terms of gains.

Social implications of transitive inference

Throughout the literature there is abundant evidence citing the importance of transitive inference skills for group living (Bond *et al.* 2002; MacLean *et al.* 2008; Weib *et al.* 2010; White & Gowan 2012). For example understanding the relationships among members of a social group could substantially decrease the number of costly encounters an individual experiences (Weib *et al.* 2010). Furthermore being able to conceptualize these relationships based on indirect evidence could save individuals the energy and time costs associated with experiencing them first hand (Weib *et al.* 2010). As group size increases the number of pair-wise encounters also increases dramatically so individuals in larger social groups would benefit most from the ability to use transitive inference to construct linear dominance hierarchies based on indirect evidence. Although basic transitive inference abilities have been demonstrated in a number of species (Davis 1992; Weib *et al.* 2010; White & Gowan 2012) several papers have compared transitive inference abilities among closely related species that differ in their degrees of sociality. For example Bond *et al.* (2002) compared Pinyon Jays, *Gymnorhinus cyanocephalus*, which live in stable social groups of 50 to 500 individuals with Western Scrub-Jays, *Aphelocoma californica*, which live in much smaller social

groups typically consisting of a pair of birds and their associated young. Beyond degrees of sociality the two bird species face very similar ecological demands and are even sympatric in much of their range. When they compared performance among the species on two cognitive tasks related to their ability to track and assess dyadic relationships they found that social Pinyon Jays outperformed their less social counterparts (Bond *et al.* 2002). The Pinyon Jays learned to track dyadic relationships more quickly and accurately than the Western Scrub-Jays. The Pinyon Jays also possessed a more accurate mechanism for transitive inference tasks. This clearly demonstrates the association between transitive inference and social complexity. Similar results have also been founded in comparisons among primate species. MacLean *et al.* (2008) compared performance on a transitive inference task between highly social ringtailed lemurs, *Lemur catta*, and less social mongoose lemurs, *Eulemur mongoz*, and found that in initial tests the ringtailed lemurs outperformed mongoose lemurs. In subsequent testing under a correction procedure designed to teach the lemurs about the underlying linearity, performance equalized indicating there was no fundamental difference in the two species ability to use transitive inference although the ringtailed lemurs were more predisposed to do so (MacLean *et al.* 2008).

Transitive inference in chimpanzees

Gillian (1981) first demonstrated transitive inference abilities in chimpanzees, *Pan troglodytes*. He used a paradigm for testing transitive inference in which subjects are trained to learn a hierarchy of stimuli and once they reach a predetermined criterion level of performance they are then tested on the novel

pairs. This has been described as the standard method for demonstrating transitive inference in animals (Allen 2006). Gillian conducted his experiment using three chimpanzees and a five stimulus series and was able to conclude that chimpanzees did have the ability to use transitive inference. Since this time no additional transitive inference tests have been conducted with chimpanzees despite the fact that they are an ideal taxon in which to study reasoning about relationships due to their complex social and nonsocial environment.

Chimpanzees live in a patrilineal society where males stay in their natal groups and females immigrate to new groups (Matsuzawa *et al.* 2006). It is characterized as a fission-fusion society meaning that all individuals are rarely present in the same area at any one time as individuals often travel and feed in smaller groups that vary in size and composition. Chimpanzee communities range in size from 15 to 150 members (Watts & Wrangham 2006). The size of these groups varies in part as a result of food availability although in general males tend to be more social than females who may often be alone with only their dependent offspring (Watts & Wrangham 2006). Communities typically have a set territory, which is patrolled by bands of male chimpanzees and females tend to stay closer to the center in core areas. Male chimpanzees form linear dominance hierarchies and competition for high dominance rank is fierce (Watts & Wrangham 2006). Females also have dominance relationships although they tend to be less rigid than males (Watts & Wrangham 2006). Chimpanzees' large group size coupled with their fission-fusion behavior and the presence of dominance hierarchies makes the ability to track and remember relationships between other individuals appear critical to

survival and reproductive success.

Chimpanzees are considered to be primarily fruit eaters or frugivores and are therefore subject to variability in food availability as it changes both seasonally and interannually (Basabose 2002). Their diets are also often supplemented with leaves, seeds, flowers, pith, bark and occasionally meat depending on the subspecies (Watts & Wrangham 2006). The seasonal changes in food availability leverage significant foraging constraints on chimpanzees in response to which they might have developed more complex cognition.

Our Study

Clearly there is an active debate as to the relative importance of social versus nonsocial factors in shaping our cognitive abilities. Both sides of the debate are represented with empirical data and correlations that support their argument. Although previous work suggests that transitive inference abilities are superior in social species—suggesting that sociality has favored the evolution of this ability—no studies have explored whether individual species are better adapted to apply transitive inference to social or nonsocial content. We compared performance on a social and nonsocial version of a transitive inference task using chimpanzees.

Methods

Study Subjects and Housing

We tested one infant (Nori, a 3 year old female) and three adult chimpanzees (Jonathan, an 17 year old male; Ruthie, a 17 year old female; and Maggie, a 40 year old female). Subjects were housed in indoor/outdoor enclosures at the North Carolina Zoo (Asheboro, NC). The chimpanzees live in typical social groups with

other individuals (average 8 individuals per group) but were separated from other subjects during testing. None of the individuals had any prior experience in related transitive inference tasks, but all subjects were trained to discriminate four pairs of images on a touch screen apparatus before beginning this study. Subjects trained to discriminate the four pairs of images until they were minimally able to complete mixed pairs trials at or above 80% correct. All testing was done while subjects were off-exhibit. All subjects had *ad libitum* access to water and were not food restricted for testing. Subjects received fresh fruit and vegetables as well as monkey chow daily. All testing occurred in subjects' home enclosures and was voluntary: data were only collected when subjects chose to approach the testing apparatus and participate in the study. This study was approved by Duke University IACUC # A078-08-03.

Apparatus

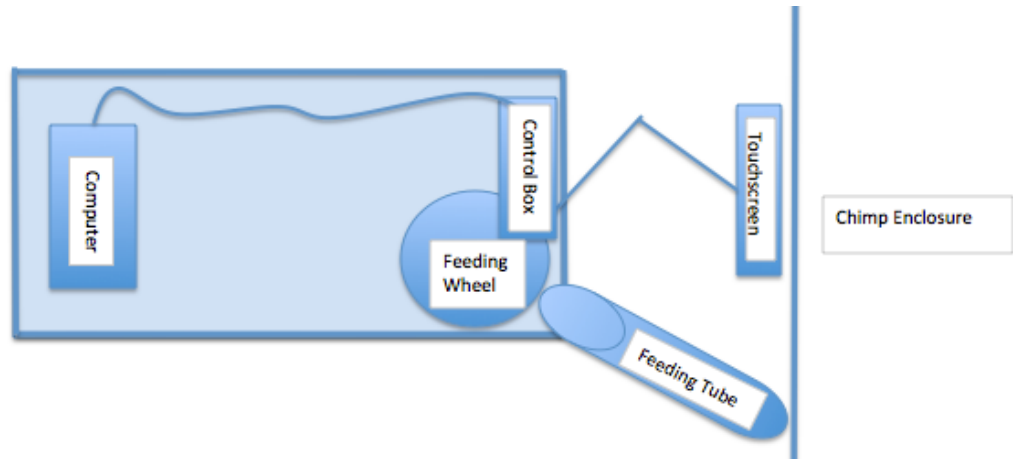


Figure 1: A bird's eye view of the testing apparatus.

Testing required subjects to make selections on a touchscreen monitor. The monitor was mounted on a mobile cart that could be pushed against the bars of the

subject's enclosure, allowing her to interact with the screen (Figure 1). The cart was also equipped with a laptop that controlled the presentation of tasks on the monitor and a Universal feeder, which automatically delivered food (small cubes of fruit from the chimpanzees' daily diet) down a tube to the subject in response to correct answers. Chimpanzees sat on the ground in front of the touch screen. A custom built VisualBasic program presented the stimuli in two central screen locations, left and right, and recorded subjects' responses. Subjects touched a small, central green rectangle to begin every trial. Correct responses were reinforced with a small cube of apple, a positive tone, a black screen and a short two second inter-trial interval. Incorrect responses elicited a warning tone and a large white X on a red screen for five seconds before proceeding to the two second inter-trial interval on a black screen. In addition, subjects received a squirt of juice at the end of each session, regardless of performance, to motivate them to complete entire sessions at a time.

Procedure

Subjects were exposed to hierarchies of 7 images and trained, using adjacent pairs, to always pick the higher ranking of two stimuli. Ultimately during the test phase of the task, subjects viewed nonadjacent pairs and were evaluated on their ability to transitively infer the higher ranking of the stimuli. To determine whether hierarchical reasoning is adapted for social or nonsocial stimuli, subjects performed the task with four separate stimuli sets. Two sets were social – pictures of unfamiliar male conspecifics – and two were nonsocial – pictures of unfamiliar fruits. All of the stimuli were unfamiliar so subject's previous preferences did not interfere with their ability to learn the presented hierarchy. Fruit was used as the

nonsocial stimuli because it is ecologically relevant. All subjects participated in the task with each of the stimuli sets in ABBA order. We counterbalanced between subjects whether the first set was social or nonsocial and whether each hierarchy was organized from A to G or G to A to ensure that intrinsic features of the hierarchy did not influence performance. A maximum of two stimuli were presented on the screen and subjects were rewarded for selecting the higher ranked stimuli. There were 30 trials in each session and the location of stimuli was counterbalanced such that each pair appeared equally frequently in the left and right locations. Additionally subjects completed as many sessions as they were willing to in any given day.

Twenty-eight color images were used throughout the study. There were 2 conditions, social and nonsocial. For each of these conditions there were two sets of stimuli consisting of seven images each. Therefore, a total of 14 images of unfamiliar adult male conspecifics were used in social conditions and 14 images of unfamiliar fruits were used in nonsocial conditions. All subjects completed all four conditions in a counterbalanced order (i.e. ABBA or BAAB). Subjects could complete as many sessions in a given day as they were willing to complete. If a subject stopped participating for five minutes or more the session was terminated. Subjects learned hierarchal ranks involving stimulus sets of 7 distinct images. Unfamiliar conspecifics and fruits were chosen as stimuli so that the hierarchical relationships that were trained in the task did not conflict with previously held hierarchies involving our stimuli. Two images were presented on the screen and the chimpanzees were required to select the higher ranking of these two stimuli in

order to receive a reward. The images were presented on the left and right sides of the screen and the location of the correct stimuli was determined randomly. We trained the chimpanzees during three distinct phases (see below) although the basic procedure remained the same throughout. Although the use of several different conditions, and particularly the comparison of social and nonsocial conditions, on a transitive inference task is novel, the general procedure is adapted from MacLean *et al.* (2008).

Training

The training subjects completed increased in complexity throughout subsequent phases until subjects learned the complete linear hierarchy.

In the initial phase of training subjects were presented with a single pair of adjacently ranked stimuli beginning with the highest ranked pair (AB). The chimpanzees were required to select the higher ranked stimuli for a reward (A) and were then able to progress to the next stimulus pairing in the ordinal sequence (BC) after performing at or above 80% correct in at least two consecutive sessions on a given pair. Chimpanzees began this phase of training with the AB pairing and progressed through all pairs in the ordinal sequence to the final FG pair.

In the second phase of training each session involved presentation of two adjacent stimulus pairs (e.g. AB, BC) but each trial still involved a single pair. Each pair was presented three times per six trials beyond which the pair presentation was semi-random. Again subjects were rewarded for choosing the higher-ranked stimulus in each paired presentation. For example session one consisted of the AB and BC pairs in which subjects had to select A in the AB pairing and B in the BC

pairing. Subjects advanced to the next grouping of adjacent pairs in the ordinal sequence after completing at least 80% of trials correctly in two consecutive sessions and concluded this phase when they met criterion on the EF and FG pairings.

In the final phase of training all sessions featured trials of all six adjacent pairs. Each pair was shown once every six trials but otherwise the order was semi-randomized. Subjects were again rewarded for selecting the higher ranked of the two stimuli presented on each trial. Each session contained 30 trials. Subjects received 66 sessions of the final training phase before advancing to the test sessions.

Testing

The test session consisted of 30 trials of familiar adjacent pairs (five trials per pair) and six probe trials of novel nonadjacent pairs (one trial per pair). The test always began with at least 6 familiar trials after which probe trials were interspersed randomly throughout the adjacent pairs trials. The probe pairs were presented once every five trials with at least two familiar trials occurring between probe trials. Probe pairs were presented in random order with the restriction that all pairs were presented once per session. As in the training phases, subjects were only rewarded for selecting the higher-ranking stimuli during trials of familiar adjacent pairs. However, there was no differential rewarding during the probe trials, i.e. both correct and incorrect choices were rewarded. All combinations were tested as probe pairs as long as they had one intervening stimulus and with the exception of the highest and lowest ranked stimuli (A and G) since these stimuli

were conditioned as either always correct (A) or always incorrect (G). This resulted in six different probe pairs. Each individual completed ten test sessions.

Data Analysis

All data (choice and latency) were collected automatically by the computer. Descriptive statistics were used to compare performance between subjects for the first two phases of training. T-tests were used to assess differences in performance and latencies between conditions for a given subject. Binomial tests were used to assess individual performance within a condition.

Results

Two subjects (Jon and Nori) successfully completed phase one and phase two of training. Jon completed the social condition, which utilized pictures of unfamiliar conspecifics, whereas Nori completed the nonsocial condition, which consisted of images of unknown fruits. Jon completed 23 sessions to complete phase one and 33 sessions to complete phase two for a combined total of 56 sessions. Nori completed 17 sessions in phase one and 26 sessions in phase two for a combined total of 43 sessions. For phase one Jon had an overall average accuracy of 74.6% correct and 73.8% correct for phase two. For phase one Nori had an overall average accuracy of 83.1% correct and 73.7% correct for phase two.

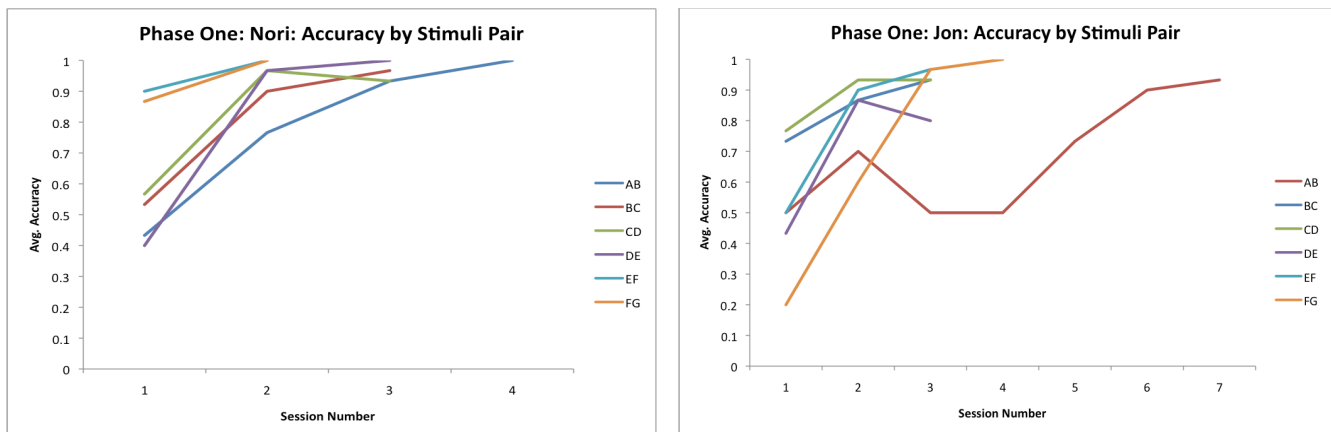


Figure 1: Average accuracy per stimuli pair across sessions in phase one.

Both Jon and Nori show learning curves for all stimuli pairs as they progress through session numbers in phase one (Figure 1). Nori appears to be learning more quickly as she required fewer sessions to complete each stimuli pair.

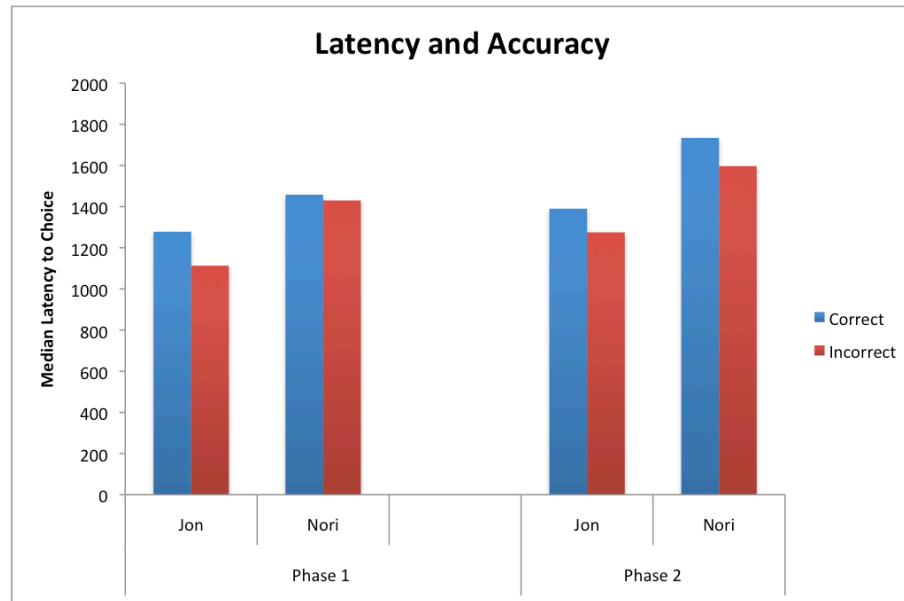


Figure 2: Median latency to choice broken down by phase, subject, and incorrect or correct responses.

Median latencies were higher for both Jon and Nori in correct trials than incorrect ones. However, overall Jon's median latencies to choice are lower than Nori's (Figure 2). When these data are further broken down by stimuli pair Jon continues to demonstrate faster median times to choice than Nori (Figure 3). Nori has a faster median time to choice than Jon on only one of the stimuli pairs, pair DE.

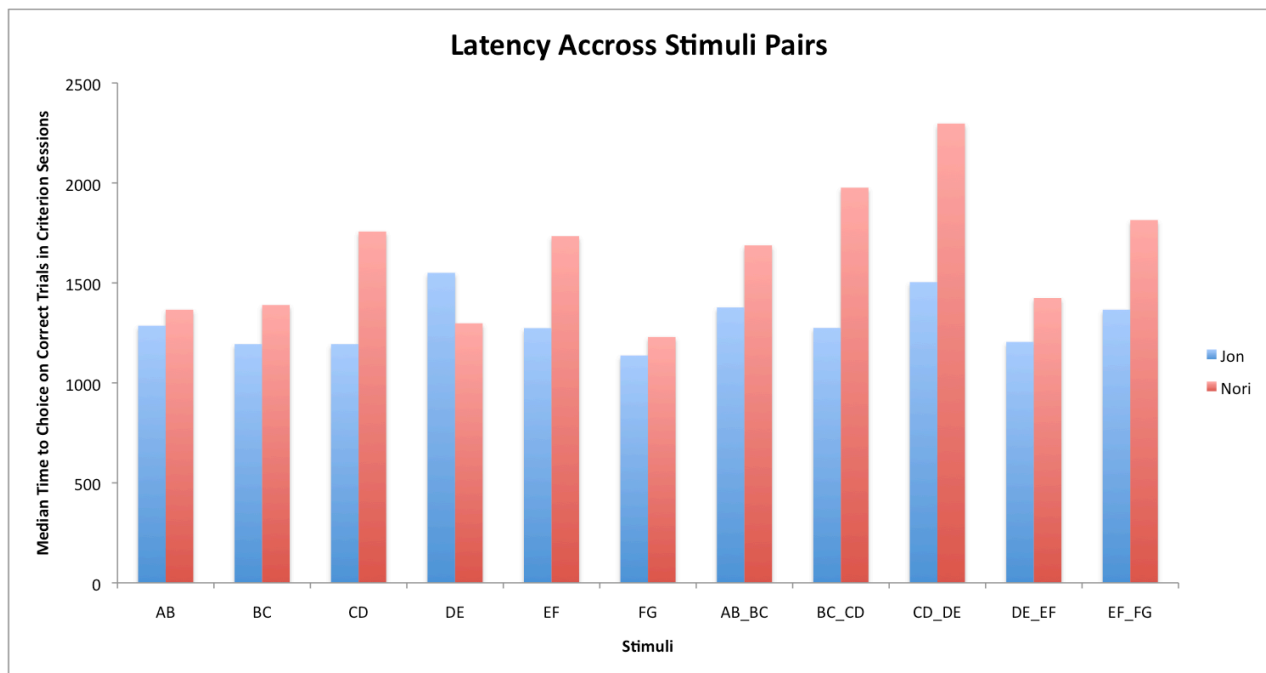


Figure 3: Median time to choice for correct trials in the criterion sessions broken down by subject and stimuli.

Discussion

In beginning this study we had three main hypotheses, which are as follows. Our first hypothesis was that transitive inference is adapted for navigating the social world. In this scenario we would predict that chimpanzees will exhibit greater performance, meaning higher accuracy and lower latency to choice, in the social condition when compared to the nonsocial condition and will learn the pairs more quickly. Our second hypothesis was that transitive inference is adapted for exploiting the physical world and in this case we would predict that the chimpanzees would perform better in the nonsocial version of the task when compared to the social version. Our third hypothesis was that transitive inference is a generally adapted cognitive skill and in this scenario chimpanzees will show similar performance on both the social and nonsocial version of the task.

Our data show that in general Jon, who completed the social condition, has a faster median time to choice when compared with Nori, who completed the

nonsocial condition. This finding provides support for our first hypothesis that hierarchical reasoning is better adapted to the social world. However, Nori achieved higher accuracies overall and advanced more quickly through training in the nonsocial condition than Jon did in the social condition. This finding, conversely, provides support for the hypothesis that hierarchical reasoning is better adapted for the nonsocial world. Unfortunately the presently small sample size did not permit the use of statistics to analyze these data. Therefore, although we have documented absolute differences in performance and latency it is unclear whether these values are significantly different. Both subjects have a higher median time to choice when they are correct, which may provide support for the conjecture that they are more likely to be correct when they take the time to actually think about it and consider their choices. This could be important as we move forward with the transitive inference part of the research in gauging whether the subjects are more quickly inferring relationships in one domain or the other.

The results presented here are additionally confounded by the differing characteristics of our subjects. First and foremost we only have two subjects, which makes statistical comparisons difficult. Second Jon is a seventeen-year-old adult male chimp whereas Nori is a three-year-old juvenile female. Jon is also the dominant male in his group and often appears distracted by group dynamics and encounters. Therefore, sex and age differences could have affected their attention and speed of learning. Sex differences in learning have been documented in wild chimpanzees (Lonsdorf *et al.* 2004). Lonsdorf *et al.* (2004) found that female chimpanzees began termite-fishing (a learned behavior) at a much younger age than

their male counterparts and that in young chimpanzees that had already acquired the skill females were more proficient than males based on the number of termites gathered per dip.

A number of future directions will serve to clarify the results presented here. In order to be able to comment on the evolution of transitive inference skills in chimpanzees it is imperative that we move forward with the rest of the study outlined in the methods. This study is the first study of its kind in that it allows us to test different conditions of transitive inference in one species to see what types of stimuli these psychological mechanisms are best adapted for. Completing the transitive inference portion of the task will provide another comparison of chimpanzees' ability to apply hierarchical reasoning to social versus nonsocial stimuli. In addition, completing this task with additional subjects will better allow us to examine any age or sex related differences that may be affecting subjects' accuracy and latency when learning the hierarchy. Every one of our subjects will also complete a total of four conditions (two social and two nonsocial), which will give us more data and increased statistical power as well as allow us to examine performance between conditions on an individual level. Because each individual will complete two social and two nonsocial conditions, we will be able to directly compare performance on each condition type controlling for an individual's tendency to pay better attention, learn more quickly or perform better on the task. These future directions will allow us to tease apart our three hypotheses and ultimately to shed light on the role of social versus nonsocial factors in shaping primate intelligence.

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References

- Aiello, L. C., & Wheeler, P. (1995). The Expensive-Tissue Hypothesis: the brain and the digestive system in human and primate evolution *Current Anthropology*, 36(2), 199-221.
- Allen, C. (2006). Transitive inference in animals: reasoning or conditioned associations? *Rational Animals*.
- Basabose, A. K. (2002). Diet composition of chimpanzees inhabiting the montane forest of Kahuzi, Democratic Republic of Congo. *Am J Primatol*, 58(1), 1-21. doi: 10.1002/ajp.10049
- Bond, A. B., Kamil, A. C., & Balda, R. P. (2003). Social complexity and transitive inference in corvids. *Animal Behaviour*, 65(3), 479-487. doi: 10.1006/anbe.2003.2101
- Byrne, R. W., & Whiten, A. (1989). Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans *Oxford Science Publications*.
- Byrne, R. W., & Corp, N. (2004). Neocortex size predicts deception rate in primates. *Proc Biol Sci*, 271(1549), 1693-1699. doi: 10.1098/rspb.2004.2780
- Chiappe, D., & MacDonald, K. (2005). The evolution of domain-general mechanisms in intelligence and learning. *J Gen Psychol*, 132(1), 5-40. doi: 10.3200/GENP.132.1.5-40
- Davis, H. (1992). Transitive inference in rats. *J Comp Psychol*, 106(4), 342-349.
- Dunbar, R. I. M. (1992). Neocortex size as a constraint on group size in primates. *J Hum Evol*, 20(469-493).
- Dunbar, R. I., & Shultz, S. (2007). Evolution in the social brain. *Science*, 317(5843), 1344-1347. doi: 10.1126/science.1145463
- Erhart, E. M., & Overdorff, D. J. (2008). Spatial memory during foraging in prosimian primates: *Propithecus edwardsi* and *Eulemur fulvus rufus*. *Folia Primatol (Basel)*, 79(4), 185-196. doi: 10.1159/000112911
- Gillan, D. J. (1981). Reasoning in the chimpanzee II Transitive inference. *Journal of Experimental Psychology*, 7(2), 150-164.
- Hare, B., & Tomasello, M. (2005). Human-like social skills in dogs? *Trends Cogn Sci*, 9(9), 439-444. doi: 10.1016/j.tics.2005.07.003
- Holekamp, K. E. (2006). Questioning the social intelligence hypothesis. *Trends Cogn Sci*, 11(2), 65-69. doi: 10.1016/j.tics.2006.11.003
- Humphrey, N. (1976). The social function on intellect. *Growing Points in Ethology*, 303-317.
- Kudo, H., & Dunbar, R. I. M. (2001). Neocortex size and social network size in primates. *Animal Behaviour*, 62(4), 711-722. doi: 10.1006/anbe.2001.1808
- Leighton, M. (1993). Modeling dietary selectivity by Bornean Orangutans: evidence for integration of multiple criteria in fruit selection. *International Journal of Primatology*, 14(2).
- Lewis, K. P. (2000). A comparative study of primate play behaviour: implications for the study of cognition *Folia Primatol*, 71(4), 417-421.
- Lindenfors, P. (2005). Neocortex evolution in primates: the "social brain" is for females. *Biol Lett*, 1(4), 407-410. doi: 10.1098/rsbl.2005.0362

- Lonsdorf, E. V., Eberly, L. E., & Pusey, A. E. (2004). Sex differences in learning in chimpanzees *Nature*, *48*, 715-716. doi: 10.1038/nature02527
10.1038/nature02528
- Machiavellian Intelligence II: Extensions and Evaluations* (1997). (A. Whiten & R. W. Byrne Eds. 2nd ed.). Cambridge, UK: Cambridge University Press
- MacLean, E. L., Merritt, D. J., & Brannon, E. M. (2008). Social Complexity Predicts Transitive Reasoning in Prosimian Primates. *Anim Behav*, *76*(2), 479-486. doi: 10.1016/j.anbehav.2008.01.025
- MacLean, E. L., Barrickman, N. L., Johnson, E. M., & Wall, C. E. (2009). Sociality, ecology, and relative brain size in lemurs. *J Hum Evol*, *56*(5), 471-478. doi: 10.1016/j.jhevol.2008.12.005
- Matsuzawa, T., Tomonaga, M., & Tanaka, M. (Eds.). (2006). *Cognitive Development in Chimpanzees* Tokyo, Japan: Springer
- Mikolasch, S., Kotrschal, K., & Schloegl, C. (2013). Transitive inference in jackdaws (*Corvus monedula*). *Behav Processes*, *92*, 113-117. doi: 10.1016/j.beproc.2012.10.017
- Milton, K. (1981). Food choice and digestive strategies of two sympatric primate species. *The American Naturalist*, *117*(4), 496-505.
- Milton, K. (1984). The role of food-processing factors in primate food choice.
- Reader, S. M., & Laland, K. N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proc Natl Acad Sci U S A*, *99*(7), 4436-4441. doi: 10.1073/pnas.062041299.
- Rosati, A. G., & Hare, B. (2012). Decision making across social contexts: competition increases preferences for risk in chimpanzees and bonobos. *Animal Behaviour*, *84*(4), 869-879. doi: 10.1016/j.anbehav.2012.07.010
- Silk, J. B., Seyfarth, R. M., & Dorothy, L. C. (1999). The structure of social relationships among female Savanna Baboons in Moremi Reserve Botswana *Behaviour*, *136*(6), 679-703.
- Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift Tierpsychologie*, *20*(4), 410-433.
- Watts, D., & Wrangham, R. (2006). Chimpanzees In D. Macdonald (Ed.), *The Encyclopedia of Mammals* London, England The Brown Reference Group
- Weib, B. M., Kehmeier, S., & Schloegl, C. (2010). Transitive inference in free-living greylag geese, *Anser anser*. *Animal Behaviour*, *79*(6), 1277-1283. doi: 10.1016/j.anbehav.2010.02.029
- White, S. L., & Gowan, C. (2012). Brook trout use individual recognition and transitive inference to determine social rank. *Behavioral Ecology*, *24*(1), 63-69. doi: 10.1093/beheco/ars136