précis of The Evolutionary and Developmental Origins of Human Thought

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This dissertation tackles a question at the core of foundational debates in cognitive psychology, developmental psychology, anthropology, linguistics, and animal behavior: what computational and representational capacities--if any--differ between humans and non-human primates? I focus on four cognitive domains which are critical to human thinking: number and mathematics, grammar and recursive sequencing, metacognition and self-reflective thought, and logical reasoning.

There have been a variety of theories which have been proposed to account for our complex, uniquely human cognitive abilities. Some have suggested that non-human animals are limited in their ability to combine thoughts in logical and abstract ways (Spelke, 2003; Penn, Holyoak, & Povinelli, 2008), the ability to represent hierarchical or recursive structures (Hauser, Chomsky, & Fitch, 2002; Fitch & Hauser, 2004), think about their own thinking (McGeer & Pettit, 2002), or abstract relations (Penn, Holyoak, & Povinelli, 2008). However, many of these theories rely on negative findings which are hard to draw conclusions from (Fitch & Hauser, 2004; Penn, Holyoak, & Povinelli, 2008). Chapters 2-5 challenge long held beliefs about what makes human thinking unique in the domains of number (Chapter 2), recursive sequencing (Chapter 3), Logical reasoning (Chapter 4), and Self-reflective thought (Chapter 5).

In each of these domains, this dissertation uses comparative methods to test non-human primates on a variety of novel tasks to catalog the primitive combinatorial and computational mechanisms that are shared with other primates. This offers one way of narrowing down which aspects of our cognition may be unique to humans and contribute to our uniquely human conceptual repertoire. Building from these primitive foundations, this work begins to investigate the ontological origins of our cognitive abilities in these domains. A crucial aspect of understanding where our uniquely human cognitive abilities come from is to examine how a human child goes from these simple foundations, like being able to represent simple sequences, to our adult understanding of concepts like language and formal grammar. Lastly, this dissertation uses cross-cultural methods to investigate the universality of these cognitive abilities, as well as to begin to understand how our western culture affects the development of these abilities.

Chapter 2: Evolutionary constraints on the development of human numerical concepts

The work that constitutes this chapter was published as:
Ferrigno, Jara-Ettinger, Piantadosi, & Cantlon, 2017, Nature Communications
Ferrigno & Cantlon, 2017, in Kaas, J. (Ed.), Evolution of Nervous Systems
Ferrigno, Hughes, & Cantlon, 2015, Psychonomic Bulletin and Review

Humans are unique in that they are the only animals with a formal, symbolic system of counting and arithmetic. However, many of the foundations for these abilities are present in non-human animals (Ferrigno & Cantlon, 2017) and prelinguistic children (Brannon, 2002). In this chapter, I present a series of studies which show the spontaneous and early developing nature of these numerical abilities. This work begins to separate the individual effects of foundational abilities present in all humans (as well as other primate species), the effects of our number cultural on number representation, the effects of maturation rate on quantity discrimination, and the effects of training on quantity discrimination. I first show that the ability to extract and use numerical information (as opposed to other quantitative dimensions like surface area) is a primitive, foundational cognitive ability which is shared with other primates. Next, I measure the developmental trajectory of quantity discrimination in infant monkeys compared to human infants and show that numerical discrimination abilities are yoked to the maturation rate of the species. Lastly, I show that although the ability to represent and use numerical information is spontaneous and early developing, there is still a significant effect of training on numerical discrimination abilities.

The first study in this chapter investigates whether the ability to represent numerical information is a primitive, foundational ability present in all humans and other primates. Although number is one way of representing quantity, there are many other quantitative dimensions that could also be used, such as cumulative surface area, or density. Although many animals have been shown to represent quantities, whether they represent *number* directly has been debated (Clearfield & Mix, 1999; Feigenson, Carey, & Spelke, 2002; Pinel et al., 2004; Cantlon & Brannon, 2007; Cantrell et al., 2015).

To address this question, I developed a nonverbal quantity categorization task which could be used to test monkeys, young children, US adults, and Amazonian adults from the Tsimane' tribe (Ferrigno, Jara-Ettinger, Piantadosi, & Cantlon, 2017). In this task, subjects could choose to categorize sets of dots using number, surface area, or a combination of the two (Figure 1a). Our results showed that regardless of age, education, or numerical culture, humans and monkeys are biased to represent and use number (see Figure 1b). This bias is then strengthened in those with formal education and exposure to counting. This work challenged previous theories that the ability to extract and use numerical information was a culturally constructed ability. Instead this work suggests that our ability to extract and use numerical information (opposed to other non-numeric quantitative information like surface area) is a widespread and likely evolutionarily ancient ability. This fundamental bias to segregate numerical information from other quantitative dimensions and *use* it preferentially was likely an important catalyst for the emergence of an abstract, discrete counting system in human cultural evolution.

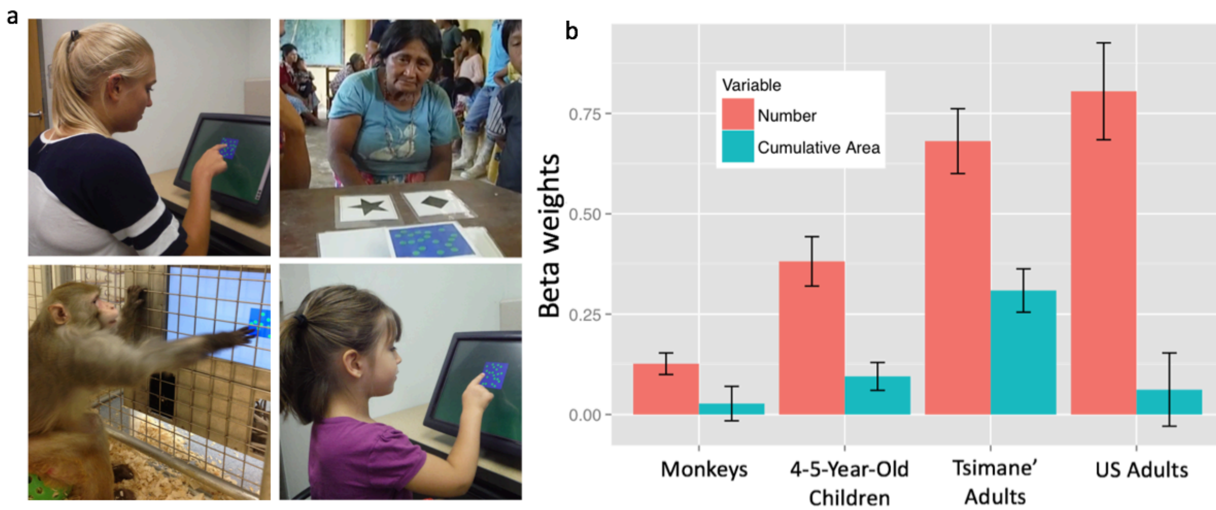


Figure 1. *US adults, Tsimane' adults, monkeys, and children on the quantity categorization task (a). Relative contributions of number and cumulative area on subjects' quantity categorization choices (b). The beta weighs show the results from a mixed effects regression predicting category choice using number and cumulative area as predicter variables (and subject as the random effects term). In all groups the number weight is significantly higher than the area weight. The error bars represent the SE of the mean.*

Although the capacity to extract and use numerical information is found both in human and non-human primates, children's numerical acuity is slow developing. One possible reason for this is due maturation or genetics. In the next study in this chapter, I used differences in species maturation rates (monkeys mature faster than human infants) to test for maturational factors in the development of quantity representations (Ferrigno et al., 2015). Infant monkeys offer a unique opportunity to test maturational factors of cognition because they mature faster due to genetic differences. Using a food discrimination task, I presented infant monkeys with two food options with varying number of items. I measured how precise the monkeys were at choosing the more numerous of the two options. I found that infant monkeys were just as precise in their quantity estimation as adult animals. Furthermore, infant monkeys could more precisely discriminate between quantities than human infants of the same age. This suggests that the approximate number system is likely yoked to the rate of maturation in primates. This research has helped the overall understanding of how our innate approximate number system develops over the course of ontogeny.

Although differences in maturation rates seem to play an important role in the development of our approximate number system, it does not rule out a role of experience. In the last section of this chapter, I measure the effects of explicit training on the precision of approximate number abilities in monkeys. I show that with extensive training (~20,000 trials), the animals were able to discriminate between sets at a 3:4 ratio. Their sensitivity nearly doubled as a result of this training. This precision is greater than the average 4-year-old child. However, even after this extensive training, the animals were far less sensitive than the average human adult, which suggests species-specific limitations on numerical learning. Overall, this work shows that primates' representations of numerosity are influenced by both the maturation rate of the species and experience with numerical discrimination.

The data in this chapter provides the first direct assessment of the relative contributions of species maturation, experience, and culture on human nonverbal number representation. I show that all three of these factors play an important role in the development of numerical abilities. Although, humans and non-human primates both spontaneously extract numerical information from visual arrays, we found an increase in this ability based on species differences, age, and culture. Additionally, I measured different contributions of the maturational and training effects on the precision of approximate number system. Taken together, this research provides strong evidence that evolutionary constraints impact the development of human numerical cognition. Evolutionary constraints are thus at the foundation of human mathematics development.

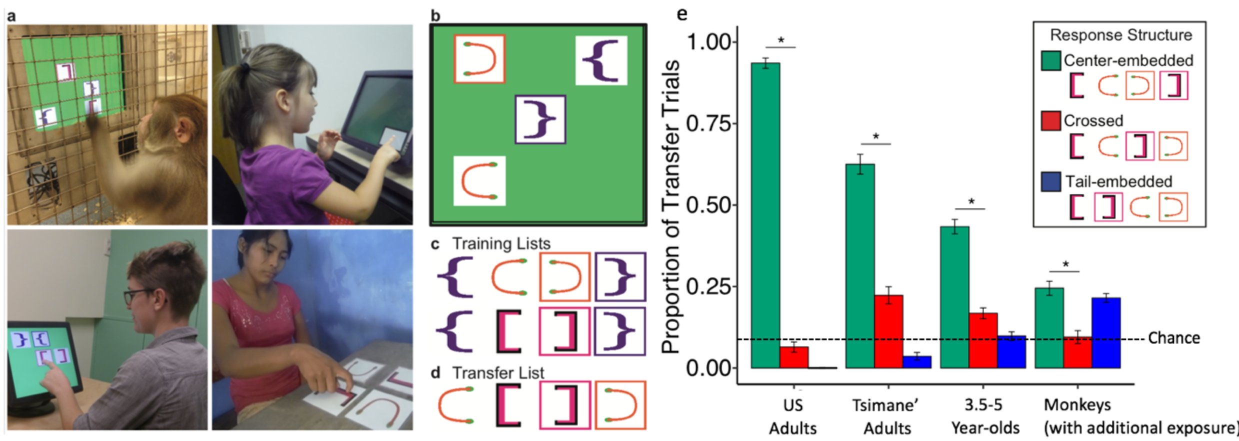
CHAPTER 3: Representation of recursive structures

The work that constitutes this chapter is currently under review as:
Ferrigno, Cheyette, Piantadosi, & Cantlon, under review

Human language is unbounded: We can create an infinite number of expressions because words and phrases can be nested inside each other. This process of nesting items within each other is called recursion. For example, in the sentence "The cat the dog chased ran", the phrase "the dog chased" is embedded inside of the phrase "the cat ran". The process used to generate these types of center-embedded structures has been hypothesized to be an important prerequisite in a number of important milestones of cognitive development such as language (Chomsky, 1957), complex tool use (Badler et al., 2000; Jackendoff, 2007), music (Lerdahl & Jackendoff, 1983), theory of mind (Jenkins & Astington, 1996), and mathematics (Hauser et al., 2002; Piantadosi et al., 2012). Additionally, the capacity to represent recursive structures has been theorized to be uniquely and universally human. However, its origins in evolution, development, and culture are controversial and largely remained untested.

In this chapter, I test whether the ability to represent recursive sequential structures is uniquely human, when this ability arises in children, and whether this ability is present across widely different cultures. To do this, I used a novel non-linguistic sequence generation task to test recursive center-embedding abilities in monkeys, children (age 3.5-5 yrs.), US adults, and Tsimane' adults who have little formal education (Figure 2a). Participants were first trained on a center-embedded sequence generation task in which they were presented with four bracket images in random locations on a touchscreen computer and had to touch them in a *specific* center-embedded order in order to receive positive feedback (e.g. "{, then [, then], then }", see

Figure 2b). Subjects were trained on two of these lists (“{ [ ] }” & “{ < > }”) until they reached the training criterion of 70% correct (Figure 2c). Once trained to criterion, a novel list, which was composed only the center two elements from each of the training lists which had never been shown together ("<", ">" & "[", "]"), was randomly mixed into training trials (see Figure 2d). Importantly, these test items occupied overlapping ordinal positions in the training lists. Both of the open brackets were presented in the 2nd position previously and the close brackets were in the 3rd position previously. Thus if subjects use an ordinal strategy based on where the items were seen in previous lists, we should see an equal mix of center-embedded structures (e.g. "([])") and a non-embedded, crossed structure (e.g. "([)]"), because both preserve the ordinal positions as closely as possible. Thus, a bias to order the pictures in a center-embedded fashion between these structures would suggest that they are representing the overall abstract, recursive structure of the lists.



We found that all human groups and monkeys spontaneously generalized the center-embedding structure to the transfer stimuli (see Figure 2e). However, children and monkeys had less consistent responding (more crossed structures) and monkeys needed additional training before generalizing the structures. These results were supported by a Bayesian data analysis which infers each individuals' and subject group's likely distribution of strategies and noise parameters. This work challenged long standing theories about what makes humans unique. It suggests that the ability to represent recursive structures is not the defining feature of human cognition, nor is it the limiting factor for learning human language.

Chapter 4: Logical reasoning

The work that constitutes this chapter is currently under review as:
Ferrigno, Huang, & Cantlon, under review

Humans can think and reason using logical concepts to flexibly make inferences based on new information. We have explicit labels for both the logical concepts as a whole (e.g. “the disjunctive syllogism” or “If A *or* B, *not* A, *therefore* B”), as well as the logical operators (e.g. “*or*”, “*and*”, & “*not*”. This capacity for logical inference is thought to be a critical aspect of human learning, reasoning, and decision- making. However, we do not understand how this ability develops. Some have theorized that this ability requires learning the explicit labels for logical operators (Mody & Carey, 2016), while others theorize that the ability to make logical inferences does not rely on language and could be present in pre-linguistic (or non-linguistic) minds (Cesana-Arlotti et al., 2018).

One simple test case for logical reasoning is the disjunctive syllogism (If A *or* B, *not* A, *therefore* B"). Although the *explicit* formation of this logic requires symbolic thought, it is possible that the underlying logic might be able to be represented non-linguistically in pre-linguistic children or non-human animals. For example, previous work has shown that non-human animals are capable of reasoning by exclusion, one aspect of the disjunctive syllogism (*not* A – avoid empty). Studies have tested a variety of animals with a two-cup hidden baiting paradigm (Call, 2004). In this task, a researcher hides a food item in one of two cups such that the animal doesn't know which cup it is in. The researcher then shows the animal that one of the cups is empty. Many different types of animals then choose the cup which was not shown to be empty (Apes: Call, 2004; olive baboons & macaques: Schmitt & Fischer, 2009; Petit et al., 2015; birds: Schloegl et al., 2009; Pepperberg, et al., 2013). However, this task cannot differentiate the difference between just avoiding an empty cup or inferring that the remaining cup *must* contain the item.

To test if a non-human animal can represent the full disjunctive syllogism, I used a 4-cup hidden food choice paradigm in olive baboons. This task allows us to rule out alternative strategies like just avoiding the empty cache (Mody & Carey, 2016). In this task, there are two sets of two cups. One set of cups was occluded and a food item is hidden behind one of the cups in that set. This was then repeated for the second set. The occluder was removed, and the monkey was shown that one of the cups is empty (and therefore the remaining cup in that set must contain the treat). If the animals are just avoiding the empty set, they should choose from the remaining 3 cups randomly. Instead, our results show that monkeys choose the cup that must contain the food item more often that chance and thus have the capability of representing the dependent relationship between the cups. This is the first evidence that a non-human primate can reason through a full disjunctive syllogism (instead of just avoiding the cup shown to be empty). These results suggest that the capacity to reason through a disjunctive syllogism is not unique to humans and thus within the capacity of a non-linguistic mind. These results add to the growing work showing what types of mental representations and computational abilities can be accomplished in the absence of language.

Chapter 5: Metacognition

The work that constitutes this chapter was published as:
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Ferrigno, Bueno, & Cantlon, 2019, Animal Behavior and Cognition

When asked a question, we can make judgments about how confident we are that we know an answer or not. We can answer with confidence, give a qualified answer, or say "I don't know".

These types of judgments are crucial for many aspects of our lives including when to seek out more information or for a student to decide whether to continue studying for a test. However, humans have incorrect intuitions about how their own memory works. This is especially true in children. Recent evidence suggests that perceptual fluency, or how easy a stimulus is to perceive, can affect how confident you are about your answer. A reliance on these perceptual cues can lead to “metacognitive illusions” when these cues are experimentally dissociated. For example, one study presented subjects with a list of words to remember. Half of the words were presented in a large, high fluency font and the others were presented in a small, low fluency font (Rhodes & Castel, 2008). When asked how likely the subjects were to remember the words, they were more likely to say they will remember the words on the later memory test when they were presented in larger font. However, this had no effect on their actual accuracy. These type of fluency effects have been seen in a variety of different tasks. However, exactly why this effect is seen is currently unknown. One possibility is that it is due to some human specific component such as an explicit belief about how our own memory works (Mueller, Tauber, & Dunlosky, 2013). Others have suggested that this is a primitive, foundational component of how memory and metamemory work (Undorf & Erdfelder, 2011).

To test whether this reliance on fluency for metacognitive judgments is a primitive mechanism, or if it is learned through human specific component, I tested whether non-human primates rely on the same mechanisms to make metacognitive decisions (Ferrigno, Kornell, & Cantlon, 2017). Like humans, monkeys can make judgments about their own memory by reporting their confidence during cognitive tasks. Some have suggested that animals use associative learning to make accurate confidence judgments, while others have suggested animals directly access and estimate the strength of their memories. Here we tested a third, non-exclusive possibility: perhaps monkeys, like humans, base metacognitive inferences based on heuristic fluency cues.

Subjects were presented with a picture to remember, took a memory test, and made either a low-risk or high-risk bets on their accuracy. The betting occurred either before (prospective) or after (retrospective) the memory test. If subjects choose the low-risk option they received a small reward regardless of accuracy on the memory task; if they selected the high-risk option they would either receive a large reward or equally large punishment based on their performance on the memory task. As has been seen with previous animal metacognition tasks, the monkeys chose the high-risk option more often when they performed accurately on the memory test. We then introduced the fluency manipulation. The images were either presented in a low fluency/contrast format (grey on a white background) or high fluency/contrast format (black on a white background). Similar to humans, monkeys showed a confidence bias based on the fluency of the stimuli even though memory accuracy was unaffected. This is novel evidence that animals are susceptible to metacognitive illusions similar to those experienced by humans. Our results show that metacognitive illusions like the fluency effect are a basic property of a primate mind, perhaps due to common evolutionary or environmental influences on cognition. This work not only challenged what we think about how monkeys make metacognitive judgements but suggests that the effects of fluency are not due to uniquely human factors as some have suggested.

Chapter 6: Conclusion

The first 5 chapters of this dissertation provide evidence that the fundamental capacities for many complex human cognitive processes are present in non-linguistic animals. However, the fact remains that humans are the only animals to create a world with complex mathematics, science, and engineering marvels. In the final chapter of this dissertation, I lay out a variety of theories which have been proposed to explain these differences. Many of these theories suggest that there is one stark discontinuity between humans and animals in a single cognitive capacity (e.g. language/recursion: Hauser, Chomsky, & Fitch, 2002; Higher order logic: Penn, Holyoke, & Povinelli, 2008; or social abilities: Tomasello & Moll, 2009). I present evidence against these hypotheses in their strongest form and offer a new hypothesis: the differences seen in humans and non-human animals may be based on a combination of multiple factors (such as our language abilities, tendency to generalize, and our unique social and cultural environment) as well how these factors interact with one another.

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