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THE END-STATE COMFORT EFFECT IN VERVET MONKEYS (*CHLOROCEBUS PYGERYTHRUS*)

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ABSTRACT

Adult humans anticipate the consequences of forthcoming actions. In second order motor planning, an individual adopts a grasp or action not just based on the immediate task demands, but in anticipation of what is going to be done next. The end-state comfort (ESC) effect is a subclass of second order motor planning effects that emphasizes terminal positions. Evidence for the ESC effect has previously been found in multiple species of nonhuman primates and there is a clear developmental trajectory to the use of ESC in humans. This study attempted to find evidence for ESC in a species on nonhuman primate not previously tested and to fill a critical gap in the literature by asking whether there is a developmental trajectory for nonhuman primate ESC akin to what is observed in human children. We tested two groups of juvenile vervet monkeys (*Chlorocebus pygerthrus*), young juveniles (aged 4-7 months) and older juveniles (15-30 months) and two mature adults. A cup-manipulation-task was used where a cup was placed in either an inverted or upright orientation and the monkeys had to pick it up in order to retrieve a marshmallow stuck inside. We expected that the monkeys who demonstrated ESC would deploy a thumb-down (inverted) grip on the stem in order to facilitate rotation of the cup and extraction of the marshmallow in a more stable and comfortable position. We found that overall, 12 out of 25 monkeys inverted their grip in at least one of the inverted cup trials thereby providing an existence proof for the ESC effect. When analyzed by age group, there seemed to be a developmental trend. The young juveniles had a lower proportion of individuals who used an inverted grip at least once relative to the group of older juveniles. The young juveniles also exhibited a higher frequency of other grips relative to the older juveniles indicating greater variability in the strategies employed to complete the task.

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Chapter 1

Introduction

Grasping an object involves planning and mentally representing the action and the goal (Rosenbaum, Herbort, Van der Wel & Weiss, 2014). These steps may be most evident in second order motor planning, in which an individual adopts a grasp or action not just based on the immediate task demands, but in anticipation of what is going to be done next. One widely used example of this phenomena is how individuals turn over an upside-down glass to pour water into it. Actors will initially grasp the cup with a thumb down posture (i.e., an initially uncomfortable position) to accommodate for the later task demands of holding the cup upright (such as while filling it). This phenomenon has also been termed the end-state comfort (ESC) effect (Rosenbaum et al., 1990), which is a subclass of second order motor planning effects that emphasizes terminal positions (see Rosenbaum et al., 2014 for further discussion). The end-state comfort effect reflects planning. It shows that when an actor deploys a grip, they are not only considering that immediate action but that grip also reflects knowledge of what the actor plans to do with that object. As the ESC effect is representative of cognitive abilities related to anticipatory motor planning skills, several studies have been devoted to documenting its ontogenetic and phylogenetic roots. The goal of this thesis is twofold: First, the study investigates the ESC effect in a species that has never been investigated before, namely vervet monkeys. Second, there is currently very little published data on the developmental trajectory of the ESC effect in nonhuman primates and consequently, this study focuses on two cohorts of very young vervets.

Second Order Planning in Human Adults and Children

Since Rosenbaum and colleagues (1990) coined the term, the ESC effect, a number of laboratory studies have studied this effect and potential modulating factors (see Rosenbaum, Chapman, Weigelt, Weiss, & van der Wel, 2012 for a review). In multiple tasks adults have been found to use initially atypical or uncomfortable initial grasps to facilitate later use of a more typical or comfortable grip (Rosenbaum, Chapman, Coelho, Gong, & Studenka, 2013; Rosenbaum et al., 2012). The first task developed to test the presence of the ESC effect in adults was the bar-transport task (Rosenbaum et al., 1990). The bar-transport task involved presenting adults with a horizontally oriented dowel with one white and one black end resting on two supports. The participants were asked to take hold of the dowel and place it in a vertical position with either its white or black end onto either a blue or red target circle to the left or right side of the supports. The task used a two-alternative forced choice method, the participants could use either use an overhand (palm-down) grasp or an underhand (palm-up) grasp. Participants were not explicitly instructed on how to grasp the dowel. The initial grasps resulted in either a comfortable thumb up or an uncomfortable thumb-down grasp at the end of the action. Using this task Rosenbaum and colleagues (1990) found that participants consistently chose an initial grasp that would facilitate a comfortable thumb-up posture when the dowel was placed on the target. Variations on the dowel-transport-task in later studies underscore the robustness of the ESC effect in adults (Rosenbaum & Jorgenson, 1992; Short & Cauraugh, 1997; Short & Cauraugh, 1999).

The dowel-transport-task and two other tasks that were originally developed for adults to investigate the ESC effect have since been used as originally conceived and adapted for use with children. The handle-rotation task was first introduced by Rosenbaum and colleagues (1993). In this task participants were asked to grasp a handle and turn it to rotate a disk 180° so a tab would line up with a given location around the disk's perimeter (Rosenbaum et al., 1993). Another task developed was the overturned-glass-task, in which participants were asked to pick up an inverted cup, turn it over and then fill it with water (Fischmann, 1997). In both of these tasks, adults use initially uncomfortable grasps to ensure a comfortable grasp at the final state of the action (Fischmann, 1997; Rosenbaum et al., 1993). These three tasks (the dowel-transport-task, the bar-rotation-task, and the overturned-glass-task) and variations upon them have also been used to study the ESC effect in children.

Children have not been found to consistently use ESC planning at adult levels until late childhood. The findings of when robust use of ESC develops in children have been inconsistent (see Wunsch et al., 2016 for a review). Some studies have found evidence for the presence of ESC in the majority of normally developing children as young as age 3, but it seems dependent on the task (Jovanovic & Schwarzer, 2011; Knudsen et al., 2012). For example, Knudsen and colleagues (2012) found that children's use of ESC increased from 13% in 3-year-olds to 94% in 8-year-olds when given a bar-transport-task (see description of original task above). That same study also found that when the children were given an overturned-glass-task, in which children were asked to pick up an inverted glass and place it right-side-up on a coaster, their use of ESC increased from 63% in 3-year-olds to 100% in 8-year-olds (Knudsen et al., 2012). In contrast to these results, Adalbjornsson and colleagues (2008) found that only 20% and 35% of children aged 2-3 years and 5-6 years showed ESC respectively when given an overturned-glass-task. Unlike Knudsen and colleague's (2012) overturned-glass-task, the children in Adalbjornsson and colleague's (2008) study were asked to pour water into the glass once it was right-side-up. While there are inconsistencies in the results of ESC effect in children, there appears to be a span of development between the ages 3-12 with a spurt in development from ages 5-8 in the majority of children (Jongbloed-Pereboom et al., 2013; Knudsen et al., 2012; Scharoun & Bryden, 2013; Stöckel et al., 2012; Thibaut & Toussaint, 2010; Weigelt & Schack, 2010, Wunsch et al., 2014).

Comalli and colleagues (2016) attempted to explore some of the reasons for inconsistencies in previous studies of ESC in children. Comalli and colleagues (2016) tested children at 4, 8 and 12 years of age with a hammering task. For the task participants were instructed to pound a peg with the hammer until the peg is flat. The hammer was placed on two blocks so participants could easily use either an overhand or underhand grip when grasping the handle. The hammer was presented with either the handle pointing to the left or right. Conditions were considered 'easy' if the hammer handle was pointing toward the participants' dominant hand or 'hard' if the handle was pointing away from the dominant hand. They recruited a larger group of 4-year-olds since they expected them to exhibit the greatest amount of variability. The children were given a total of 20 trials each, 10 'easy' and 10 'hard'. Comalli and colleagues (2016) found high inter- and intra-individual variability in the initial grips children produced in the hard condition.

Comalli and colleagues (2016) performed a second experiment in which they prevented the children from using their non-dominant hand to complete the same hammering task by placing an oven mitt on that hand. By preventing use of the nondominant hand they made it more difficult and awkward to change an initial grip. With these restrictions children's use of ESC increases (Comalli et al., 2016). In that task some of the children do manage to adjust their grips if their initial grip is not an efficient way to complete the task, but there was a trend towards using an ESC grip across trials (Comalli, et al., 2016). The results of this experiment indicate that children were able to learn within a single session to avoid an inefficient grip when it is shown to be more costly.

Notably the age groups showed levels of ESC consistent with previous studies. The novel finding within this study is the level of intraindividual variability in the youngest age group and the changes in this variability across development. The young children tested by Comalli and colleagues (2016) showed that they can produce initial grips consistent with ESC, but that strategy is not prioritized in their responses. When children used an initial grip inconsistent with ESC most proceeded to change their grip. When changing the grip they almost always transitioned from a non-radial to radial grip, the radial grip being the most efficient way to grip the hammer in order to pound the peg (Comalli et al., 2016). The second experiment indicated that when the ability to change the initial grip is more costly the 4-year-olds demonstrated ESC planning more frequently. The high level of variability aligns with hypotheses from Siegler (1989, 1994, 1996) that stress variability is a necessary aspect to learning better strategies, with variability being highest in early learning and decreasing as experience increases. Thus, low levels of ESC found in children could be indicative of early learning and the testing of alternative strategies by individuals. Additionally, the results of the second experiment indicate that when the costs are high enough the prioritization of efficient strategies can happen quickly. However, studies need to be done with greater numbers of trials and analyses that include multiple grip types in order to investigate the variability within these populations.

Second Order Planning in Nonhuman Primates

Contrasting research with human children, relatively few studies have investigated second order planning in nonhuman primates. This line of research is important as it can inform the phylogenetic roots of second order planning within the primate lineage. It had been argued previously that motor planning for future body states and the cognitive abilities tied to that type of planning provides sufficient and necessary conditions for tool-use (Johnson-Frey, 2004). If that was the case non-tool-using primates should not show the ESC effect or second order planning. By using a comparative approach and studying both tool using and non-tool using primates we can gain a deeper understanding of the cognitive abilities required for advanced tool-use and the evolutionary roots of motor planning in the primate lineage.

In order to test a non-tool-using primates' ability to use second order planning, Weiss and colleagues (2007) sought evidence for the ESC effect in cotton-top tamarins, a small, arboreal New World Monkey species that are not believed to use tools in the wild. The ability to learn means-end relationships related to tool-use had previously been found in captive tamarins, suggesting that they have one of the cognitive prerequisites necessary for ESC (Santos et al., 2006; Santos et al., 2005). To test if tamarins depart from their normal preferred mode of grasping in order to accommodate a future state, they were presented with two different experimental conditions. In the first experiment the tamarins were presented with an inverted or upright cup (a plastic champagne glass with a stem modified to accommodate the hand size of the tamarins) with a marshmallow inside. The cup was placed in an apparatus that required it to be removed by the stem in order for the tamarin to access the marshmallow. The grips with which the tamarins grasped the stem in the upright-cup condition or the inverted-cup condition were the variables of interest. If the tamarins grasped the stem with a thumb-up grip in the upright condition but a thumb-down grip in the inverted condition it would indicate that they are planning for future body states when manipulating objects (Weiss et al., 2007).

The tamarins were given 2 trials per cup orientation (upright or inverted). They grasped the stem with a thumb-up grip in all upright-cup trials. In the inverted cup trials, they grasped the stem with a thumb-down grip in 15 out of 18 trials. These results were consistent with what would be expected if the tamarins were demonstrating the ESC effect. A second experiment was done with the tamarins in order to check that the behavior observed in the inverted cup trials was not due to simple behavioral associations of associating common (thumb-up) grips with the upright cup conditions and uncommon (thumb-down) grips with the inverted condition. In this condition Weiss and colleagues (2007) replaced the vertical stem of the cup with a horizontal U-shaped handle in order to see if the use of the ESC effect would generalize to a task involving a novel handle shape. The procedure for the second condition was identical to the first condition. Weiss and colleagues (2007) postulated that the results would be consistent with the tamarins demonstrating the ESC effect if they used an overhand (palm-down) grasp when the cup was in an inverted position and an underhand (palm-up) grasp when the cup was in an upright position. They found that the tamarins used an overhand (palm-down) grasp in all of the inverted cup trials. In the upright cup condition, the tamarins used an underhand (palm-up) grasp in 12 of 16 trials (one monkey was excluded for consistently using the rim to remove the cup from the apparatus in the condition). Overall, the results of both experiments indicate that tamarins demonstrate the ESC effect and second order planning at a robust rate (Weiss et al., 2007).

In order to further explore the phylogenetic and evolutionary roots of second order planning and the ESC effect, Chapman and colleagues (2010) tested lemurs, the most evolutionary distant primate relative to humans. A slightly modified version of the task Weiss and colleagues (2007) used with the tamarins was given to six species of lemur. The lemurs were given three trials each in two conditions, an upright cup condition and an inverted cup condition. The main difference between Weiss colleagues' (2007) experimental set up and Chapman and colleagues' (2010) was that the cup was not placed in an apparatus when the lemurs were tested. Instead, in the inverted condition the cup was just placed in an inverted fashion with the bowl facing down on a flat surface. In the upright cup condition, the baited cup was placed with the bowl facing upright at about a 45-degree angle with the cup leaning against a wall or corner for support. All lemurs tested used an upright grasp in all upright cup trials. In the inverted cup trials 10 out of 14 lemurs used an inverted grasp at least once. The lemurs used an inverted grasp in 16 out of the 42 inverted cup trials (Chapman et al., 2010). While the majority of the lemurs inverted their grasp at least once during the inverted cup trials, the proportion of trials in which their grasps were inverted was low compared to the tamarins (Chapman et al. 2010; Weiss et al., 2007). This difference in the frequency of inverted grips could potentially be due to the lemurs being tested in a more naturalistic and less controlled setting than the tamarins.

Second order planning and the ESC effect have also been studied in primates using other tasks. Nelson and colleagues (2011) tested rhesus macaques using a spoon-reaching task adapted from one used with human infants (McCarty et al., 1999). In the task monkeys were presented with a spoon baited with food resting on bookends which left the middle part of the spoons accessible to be grasped. Three out of seven monkeys alternated their reaching hand in order to bring the bowl of the spoon to their mouth efficiently and another three monkeys changed their posture to accommodate an efficient grip with their preferred hand. Overall, the monkeys in this study resembled older infants that originally adjust their mistakes before eating the food, but with further experience they ultimately were able to efficiently transport the spoon in a single movement when it was placed in different orientations by using the strategies described above (McCarty et al., 1999; Nelson et al., 2011). These results indicate that rhesus macaques are capable of anticipatory motor planning, but in the task presented it was only demonstrated after repeated experience with the task.

Chimpanzees have also been tested to see if they demonstrate the ESC effect and second order planning. Frey & Povenelli (2012) conducted two tool-use experiments with chimpanzees in order to see if they demonstrate ESC. The first experiment was a variation on the dowel-transport-task in which one end of a dowel was baited with food. In the task the chimpanzee would pick up the dowel and bring the baited end to their mouth. The apes were given two conditions, one in which both ends of the dowel were baited so the grip choice wouldn't matter (control condition) and one in which only one end of the dowel was baited such that a grip that placed the thumb side of their hand toward the baited end would be consistent with anticipatory planning. The apes grasped the dowel in a variety of ways including over-hand, under-hand, pincer grips and grips between fingers. Despite this variability across all individuals tested each ape exhibited consistency in their chosen grasp they used regardless of experimental condition. In the first experiment no statistical significance was found between grip preferences in the control versus testing conditions, potentially suggesting that the apes don't use anticipatory planning. In order to test this hypothesis further, Frey & Povenelli (2012) conducted a second experiment in which the only way to retrieve a food reward was if the apes grasped the dowel with the thumb-side of their hand toward its center. After grasping the dowel, it had to be inserted through a hole in a Plexiglas barrier in order to dislodge a food reward. In this tool-use task all of the apes exhibited a high degree of anticipatory planning. Why did the chimpanzees show a high level of second order planning on the tool-use task but not the self-directed dowel task? One possibility posed by Frey & Povenelli (2012) was that anticipated motor costs of placing their thumb toward or away from the baited end of the dowel in the first experiment were not sufficient to influence grip selection.

All the primate species discussed thus far have found some degree of evidence for second order motor planning abilities and the ESC effect, but there is considerable variability in performance across these species. To explain this variability Zander and colleagues (2013) proposed the morphological constraint hypothesis. In previous studies the primates with limited manual dexterity, namely the tamarins and lemurs, tended to show ESC more consistently than the other primates tested. Specifically, lemurs and tamarins are restricted to use of whole hand power grips and are not capable of precision grips in which objects can be grasped between the finger and thumb (Napier 1960; MacNeilage 1991; Zander et al., 2012). For species with a lack of dexterity and limited grasping postures the costs of not adopting a grasp that accommodates future postures may be greater as they have limited ways to subsequently compensate. Likewise, species with greater manual dexterity may be able to employ numerous strategies in order to compensate for adopting a suboptimal initial grip.

To explore the impact of differences in manual dexterity on the consistency of the ESC effect and second order planning, Zander and colleagues (2013) tested two species of New World Monkeys, tufted capuchin monkeys and squirrel monkeys. Capuchins had previously been shown to use precision grips and maintain greater control in gripping relative to squirrel monkeys (Costello & Fragaszy, 1988; Welles, 1976). The apparatus and cup used by Zander and colleagues' (2013) to test both species was largely similar to Weiss and colleagues' (2007) study with tamarins, except the cup stems were modified to accommodate the hand sizes of the two species tested. Six squirrel monkeys and 10 capuchin monkeys were tested. Both species were given three test phases with two trials each. In the first phase the cup was placed in an inverted position on a flat surface in their enclosure. The second phase involved the cup in an upright position in the apparatus modelled of the one used in Weiss and colleagues' (2007) study and the last phase involved the cup in an inverted position in the apparatus. Twelve supplemental trials over three consecutive testing days were given to monkeys that did not show second-order motor planning in the first set of trials. All but one of the squirrel monkeys managed to remove the cup by grasping the bowl when it was in the inverted condition in the apparatus. Conversely, when the cup was in the inverted position on a flat surface in the first test phase the monkeys used the stem and inverted their grasp in 9 out of 10 trials. In the first test phase, the capuchins inverted their grasp in 6 out of 20 trials. When the cup was inverted in the apparatus in the third test phase none of the capuchins used an inverted grasp to remove the cup. Due to only four of the capuchins inverting their grasp in the inverted cup conditions they were all given supplemental testing trials. In the supplemental trials the capuchins inverted their grasp in 20%, 10% and 25% of the total trials on supplemental days 1, 2 and 3, respectively. Only the monkeys that had previously inverted their grasp in the initial trials inverted their grasp in the supplemental trials (Zander et al., 2013).

These results indicate that while both species are capable of second order motor planning and demonstrating the ESC effect, the rate at which it is expressed is variable. Zander and colleagues (2013) noted that the results of this study were consistent with the hypothesis that primates that are incapable of precision grasps and that seem to have less manual dexterity overall tend to show second order motor planning more consistently. The consequences for movements that are not consistent with ESC and second order motor planning appear to differ across species that have varying levels of manual dexterity. Overall, the limited research on the

ESC effect and second order planning in nonhuman primates indicates that species with lower manual dexterity tend to show the ESC effect more consistently than species with higher manual dexterity indicating that morphological constraints play a significant role in the expression of this effect (Chapman et al, 2007; Frey & Povenelli, 2012; Nelson et al., 2011; Weiss et al., 2007; Zander et al., 2013).

Current Study

We sought evidence for the ESC effect in vervet monkeys (*Chlorocebus pygerthrus*), a species that has not yet been tested. Vervet monkeys are a species of Old World monkey native to a large area of eastern and sub-Saharan Africa. They are habitat generalists as evidenced by their widespread range in Africa (Wolfheim, 1983). Vervet monkeys are non-tool-users but they have been shown to distinguish functionally relevant aspects of tools (Santos et al., 2005). Vervets have previously been shown to use precision grips when foraging, indicating they have a high level of manual dexterity (Harrison & Byrne, 2000).

The ontogeny of the ESC effect in humans is well studied, but as of yet only one study on nonhuman primates has included an infant or juvenile. Chapman and colleagues (2010) previously found that a 4-month-old infant lemur demonstrated use of the ESC effect, indicating that in lemurs use of ESC potentially develops before adult-like manual control and dexterity. Thus, a critical feature of the current study is that juveniles were tested to provide insight into the ontogeny of this phenomenon in vervet monkeys. There were several research questions of interest. The first is if vervet monkeys engage in the use of ESC. Second, whether the amount of ESC we observe changes over development. And lastly, in an exploratory analysis, to determine if there is high intraindividual variability within the initial grips akin to what is seen with young children (Comalli et al., 2016). Two groups of juveniles, young juveniles (aged 4-7 months), older juveniles (aged 18-30 months) and two adults are included in this study. The adult female, Pilani, is missing her left arm and she provides a case study for how a morphological constraint could impact the use of ESC in an adult of this species.

If we were to see higher rates of ESC use in the older juveniles compared to the young juveniles it would suggest that there could be a developmental trajectory to the ontogeny of ESC in vervet monkeys as is found in humans. This could also be evidenced if the young juveniles show more intra-individual variability in their initial grips relative to the older juveniles. If the level of intra-individual variability across age groups decreases this would parallel the results found in human children and thereby potentially indicate early learning and the testing of alternative strategies by the younger cohort (Comalli et al., 2016). Vervet monkeys are also the first species tested using the cup task that have relatively high dexterity but are not native tool-users. Capuchins, the only other nonhuman primate species with relatively high dexterity tested using the cup task are also native tool-users (Zander et al., 2013). Support for the morphological constraint hypothesis would be indicated if overall the vervet monkeys show levels of ESC consistent with other nonhuman primate species with high manual dexterity (i.e. capuchins, rhesus macaques and chimpanzees). Since only two adults were tested, it will be difficult to draw conclusions based on comparing performance across species in regard to the morphological constraint hypothesis. However, Pilani has a disability affecting her ability to subsequently compensate if she initially uses a grasp that is inefficient or ineffective to complete the task. Because of this she might provide insight as a case study related to how a nonhuman primate's use of second order planning could be impacted by a morphological constraint.

Chapter 2

Methods

Subjects

Twenty-five vervet monkeys in three different age groups were tested. The youngest group (hereafter *young juveniles*) were 4-7 months in age and were born during the 2018 breeding season. The young juveniles comprised 17 monkeys (7 males, 10 females). The second group of juveniles tested (hereafter *older juveniles*), were 15-30 months in age and were born during the 2017 breeding season. The older juvenile group comprised 6 monkeys (4 males, 2 females). Additionally, two mature adult monkeys were tested, one female (age unknown) and one male (10yo).

The vervet monkeys lived at Bambelela Wildlife Care and Vervet Monkey Rehabilitation NPC in Limpopo Province, South Africa. All monkeys in the study came to Bambelela as orphans or rescues. The juvenile monkeys tested were in rehabilitation and expected to be released back into the wild in approximately four to five years. The two adults tested were permanently housed at Bambelela due to epilepsy (adult male) and multiple limb amputations (adult female). Use and care of the vervet monkeys conformed to rules and regulations of the IACUC at the Pennsylvania State University.

Stimuli and Apparatus

The juvenile monkeys from both groups were tested in an outdoor room attached to the enclosure in which they were housed. Shade netting was placed over the fence connecting the testing room with their home enclosure in order to prevent visual access between conspecifics in the enclosure and the individual being tested. Pilani (adult female) was not isolated during the experiment and was tested in her enclosure in the presence of her cagemates. Apstert (adult male) was tested in the pre-entry area of his enclosure. While testing, the other monkeys in the enclosure did not have access to the pre-entry area but the activities could be viewed through the fence. Staff, volunteers and wild monkeys were occasionally outside the fence of testing areas while testing was taking place.

A plastic champagne glass was used for testing all monkeys (Figure 1). For both groups of juveniles, the bottom of the cup was cut off and extended with a dowel rod and duct tape. The dowel stem of the cup measured 2.5 in. in length and 0.25 in. in diameter in order to accommodate the hand size of the juvenile monkeys. The mouth of the cup was 3.5 in. in diameter and 1.5 in. deep. The cup used with the two adult tested was not extended with a dowel, instead the plastic stem was kept in place. The plastic stem was 2.75 in. long and 0.75 in. in diameter, the diameter and depth of the cup remained the same. For each trial, a small piece of marshmallow was stuck to the bottom of the cup. All trials were filmed with a FujiFilm FinePix XP130 mounted on a tripod.

Figure 1. Baited cup with manipulated stem for juveniles in testing condition (A) and control condition (B)

Procedure

All monkeys except Pilani[1] were given familiarization sessions prior to the start of testing in order to familiarize them with the transparent champagne glass. For familiarization sessions and trials the monkeys were transported to the testing area from their enclosure through the connecting gate by the experimenter. At the start of familiarization sessions, the monkeys watched the experimenter bait the cup with a piece of marshmallow. The experimenter either handed the cup to the monkeys with the stem facing the subject or placed it in front of the monkey with the stem facing them. The monkeys could pick up the cup and access the marshmallow in any way they chose. The experimenter baited the cup again once during a single session if the monkey successfully retrieved the marshmallow. These informal familiarization sessions were continued until subjects successfully retrieved the marshmallow from the cup twice. Every monkey (besides Pilani) was provided with 1 to 3 familiarization sessions. The average number of familiarization sessions per monkey was 2.16.

Following the familiarization sessions, the monkeys began testing trials. In the testing condition the cup baited with the marshmallow was placed in an inverted position with the opening facing down on a flat surface (see Figure 1a). The experimenter would then retrieve the monkey from their enclosure and carry them over to the testing area through the adjoining gate. The monkey was set on the ground and could then retrieve the marshmallow from the cup. The experimenter would then wait for the monkey to drop the cup in order to retrieve it, take the cup into an adjoining room and bait it again with food. Once the cup was baited, the experimenter

[1] Pilani was not given familiarization due to her being tested while still inside the enclosure with other conspecifics. She was also the most reluctant individual to approach the experimenter and take the cup. Considering these issues, Pilani was just provided with testing conditions in which she saw the cup baited with the marshmallow and placed in an inverted position in front of her. She did not demonstrate any issues understanding the transparent container (i.e. trying to grasp or eat the marshmallow through the transparent container).

brought the cup back into the testing room where the monkey was present, and the cup was placed back in an inverted position and the monkey was again able to retrieve the marshmallow. An attempt by the experimented to adjust their natural grip when placing down the cup in an inverted position was not made, as such it can't be guaranteed that the monkeys did not see the experimenter use an inverted grasp when placing the cup down in an inverted position. Initially, three trials were completed in the testing condition. No more than 3 trials were provided per day in each condition, and thus a maximum of 6 trials overall. Monkeys received 9 additional trials spread across three additional testing days if they did not use an inverted grip within the first three trials. Due to the variable schedule at the sanctuary, testing times varied and sessions often did not occur on consecutive days. Testing was completed over the course of 4 weeks in April 2019.

The experimenter attempted to repeat testing and control trials if the monkey did not use the stem to pick up the cup during trials. Other grips most often consisted of the monkey using two hands on the bowl to pick up the cup. This led to testing being stopped with four young juveniles, Babs, Darko, Jabulani and Mary Lou. This decision was made due to limited testing time at Bambelela and an attempt to focus on getting trials from monkeys that would use the stem in order to get data that could be used in analysis. Restricting analysis to trials in which monkeys use the stem is consistent with previous studies on ESC in monkeys (see Chapman, Weiss & Rosenbaum, 2010; Zander, Weiss & Judge, 2013).

After testing trials were completed, the juvenile monkeys were given three control trials. In the control trials the cup was placed in an upright position by suspending it on two dowel rods suspended from the fence of the testing room (Figure 1b). In order to block direct access to the bowl and marshmallow the experimenter placed a hand over the opening of the cup (see

Chapman, Weiss, & Rosenbaum, 2010). Three control trials were completed with trials repeated if the monkeys picked up the cup without using the stem, as in test trials.

The adults, Pilani and Apstert, were not given control trials due to constraints of the setting in which they were tested and time constraints on testing. In both cases the adults were tested in a different setting from where the control trials with juveniles were completed. In Pilani's enclosure there was no area in which the cup could be placed upright where she could not access the top of the cup directly. Due to her wariness of humans, it was unlikely she would take the cup while the experimenter's hand was over the opening. Apstert was not given control trials due to time constraints and the difficult logistics of finding a space to accommodate these trials.

For each trial, coders rated grip type, noting whether an inverted (thumb-down) or upright (thumb-up) grasp was deployed, or an *other* grip if the cup stem was not grasped to retrieve the marshmallow. All videos were coded by two independent coders with a Cohen's kappa of 0.82 for grip type. In both the testing and control trials, the monkeys were able to retrieve the marshmallow in any manner they chose.

Chapter 3

Results

There were 200 testing trials from 25 monkeys (17 young juveniles, 6 older juveniles and 2 adults) and 58 control trials from 19 monkeys (13 young juveniles and 6 older juveniles). Twelve additional trials were excluded from analysis due to the grip choice being occluded from the camera.

The initial grips used to pick up the cup were coded by two independent coders. These grips were coded as inverted if the monkey's hand was in a thumb-down position when initially grasping the stem of the cup as seen in Figure 2a. An upright grip was coded if the monkey grasped the stem with a thumb-up grasping posture as can be seen in Figure 2b. If the monkey used a grasp other than the two described above it was coded as *other*. Most other grips involved the monkey using a two-handed grasp on the bowl of the cup.

Figure 2. Examples of (A) an inverted grip during testing trial and (B) an upright grip during testing trial

Overall, 12 out of the 25 monkeys tested inverted their grasp at least once during testing trials (Table 1). When separated by age group, 29.4% of young juveniles and 83.3% of older juveniles inverted their initial grip *at least once* during testing trials. This difference was found to be statistically significant (p=0.022, two-tailed z-test for proportions).

Table 1. Testing trial information: Age group, number of familiarization sessions, total number of testing trials and proportion of grip types per monkey.

Monkey	Age Group	Fam. Sessions	N Trials	Prop. Inv.	Prop. Upright	Prop. Other
Babs	Young Juvenile	3	3	0	0	1
Caydon	Young Juvenile	2	3	0.333	0.667	0
Chrislin	Young Juvenile	2	13	0	0.923	0.077
Daphne	Young Juvenile	1	4	0.5	0.25	0.25
Darko	Young Juvenile	3	3	0	0	1
Ginge	Young Juvenile	2	12	0	1	0
Gira	Young Juvenile	2	12	0	0.917	0.083
Jabulani	Young Juvenile	3	6	0	0.167	0.833
Jipko	Young Juvenile	2	9	0	0.643	0.357
Lika	Young Juvenile	2	12	0.083	0.667	0.25
Maja	Young Juvenile	3	6	0	1	0
Mary Lou	Young Juvenile	3	3	0	0	1
Melane	Young Juvenile	2	7	0.286	0	0.714
Nelson	Young Juvenile	2	3	0	1	0
Oki	Young Juvenile	2	13	0	0.923	0.077
Patrick	Young Juvenile	3	7	0	1	0
Tildy	Young Juvenile	3	3	0.667	0.333	0
Abu	Old Juvenile	2	12	0.167	0.833	0
Atlas	Old Juvenile	3	12	0.167	0.833	0
Gus Gus	Old Juvenile	2	12	0.083	0.917	0
Jax	Old Juvenile	2	3	0.667	0.333	0
Menage	Old Juvenile	1	12	0.167	0.833	0
Stevie	Old Juvenile	3	11	0	0.909	0.091
Apstert	Adult	2	7	0.143	0.286	0.571
Pilani	Adult	0	7	0.714	0.286	0

In the first 3 testing trials, young juveniles inverted their grasp 10.6% of the time, while older juveniles inverted their grasp in 11.1% of the first 3 trials. This was not a significant difference with $p>0.05$. The proportion of grip types in the first 3 trials for all monkeys can be seen in Fig. 3. Three of the juveniles inverted their grip in at least one of the first 3 trials (two young juveniles and one older juvenile), whereas two juveniles (one young juvenile and one older juvenile) inverted their grip in at least 2 of the 3 trials.

Monkeys that did not invert their grip in the first 3 testing trials and used the stem to pick up the cup in at least 1 of the 3 trials were given additional testing trials. 11 of the 17 young juveniles and 5 of the 6 older juveniles were given additional testing trials. Of the young juveniles given additional testing trials only one inverted their grip in at least one of the additional trials. Four of the 5 older juveniles inverted their grips in 1-2 of the additional trials. Aggregating across the additional trials, the young juveniles inverted their grip in 3.89% of the 77 additional trials and older juveniles inverted their grip in 15.9% of 44 additional trials (Fig. 4). The difference between the proportion of inverted grasps across the two groups in the additional trials was statistically significant ($p=0.02$, two-tailed z-test for proportions).

Two young juveniles and one older juvenile inverted their grips in 50% or more of trials (Table 1). However, their total number of testing trials was low due to prioritizing additional trials for monkeys that did not invert their grips during the first three trials. This was due to time constraints on data collection. Other grips were used by 11 out of 17 young juveniles and 1 out of 6 older juveniles ($p = 0.042$, two-tailed z-test for proportions).

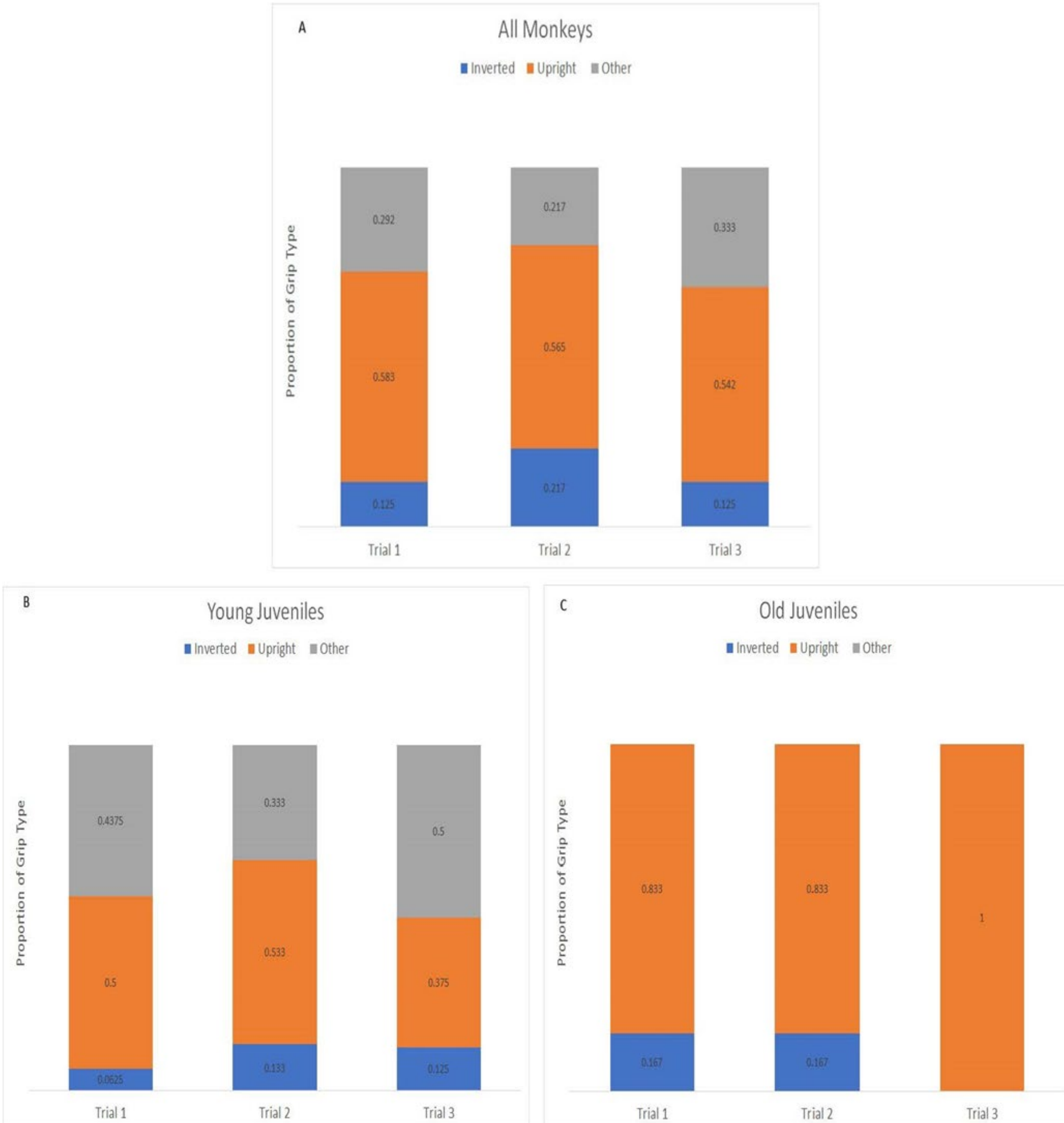

Figure 3. Proportion of grip types used within the first 3 testing trials (A) Proportion of grip types used in testing trials 1, 2 and 3 by all monkeys n=25 monkeys (B) Proportion of grip types used by young juveniles in testing trials 1, 2 and 3 n=17 monkeys (C) Proportion of grip types used by older juveniles in testing trials 1, 2 and 3 n=6 monkeys

The two adults tested each received 7 testing trials. The adult male (Apstert) used other grips 57.1% of trials, inverted in 14.3% and upright in 28.6% of his trials. Apstert demonstrated difficulties with the transparent container throughout testing (e.g., attempting to grab or eat the marshmallow through the container). The adult female (Pilani) was missing her right arm and left leg. Pilani inverted her grasp in 71.4% (5 of 7) of testing trials. In the other 2 testing trials she used an upright grip on the stem and rotated her wrist until her thumb was pointing downward and the bowl accessible to her mouth.

None of the individuals inverted their grasps during the control condition. The monkeys used an upright grasp in 93.1% of control trials. Other grips were used in the remaining 4 (out of 58) control trials. These grips were used by three young juveniles and one older juvenile in one trial each. 10 young juveniles and 5 older juveniles used an upright grip in all control trials.

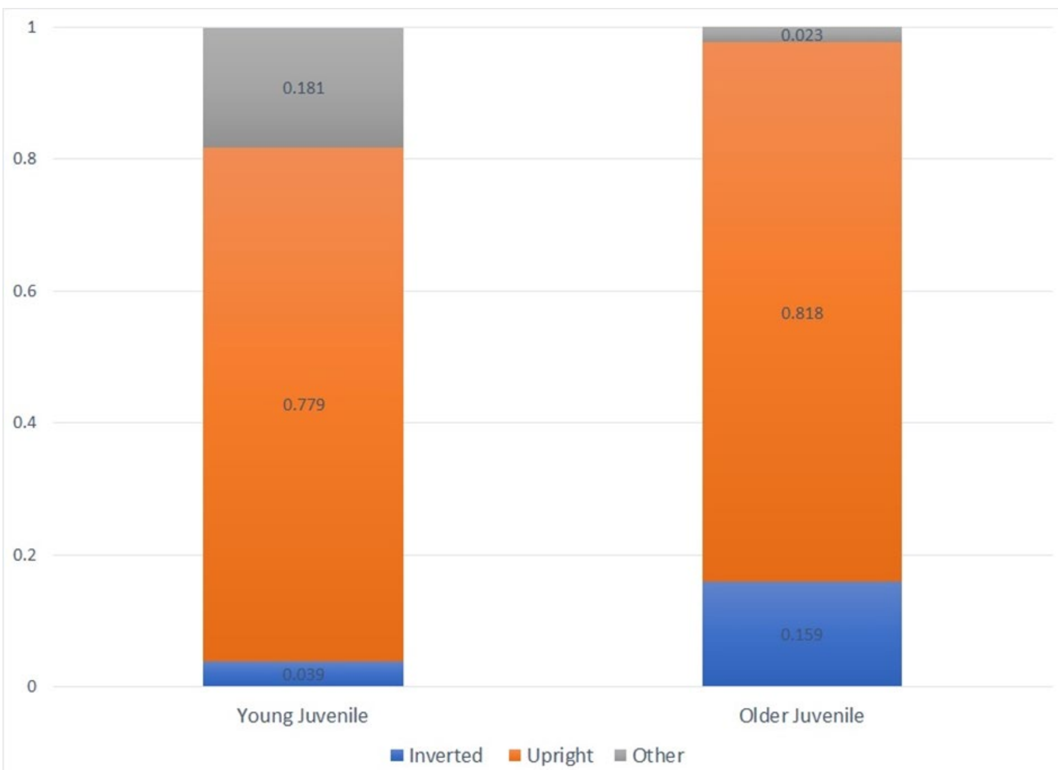

Figure 4. Aggregate proportions of grip type used in the additional trials (trials 4-12) by age group, young juvenile n=11, older juvenile n=5

Chapter 4

Discussion

The goal of this thesis was to investigate the ESC effect in vervet monkeys in order to determine if non-tool using nonhuman primates with relatively high dexterity exhibit ESC as measured by the cup task. Further, this study fills in a critical gap in the literature and asks whether there is a developmental trajectory for nonhuman primate ESC akin to what is observed in human children (e.g., Comalli et al., 2016; Wunsch et al., 2014). Consequently, two groups of juveniles, aged 4-7 months and 15-30 months at the time of testing, as well as two adults, were tested. We used a cup task that was largely analogous to methods previously used to demonstrate the ESC effect in nonhuman primates and the developmental trajectory of ESC in humans (Chapman et al., 2010; Weiss et al., 2007; Wunsch et al., 2014; Zander et al., 2013). A cup was placed in either an inverted or upright orientation and the monkeys had to pick it up in order to retrieve a marshmallow stuck inside. The dependent measure was the initial grip type used to pick up the cup. In the inverted cup condition, we expected that the monkeys who demonstrated ESC would deploy a thumb-down (inverted) grip on the stem in order to facilitate rotation of the cup and extraction of the marshmallow in a more stable and comfortable position. We found that overall, 12 out of 25 monkeys inverted their grip in at least one of the inverted cup trials thereby providing an existence proof for the ESC effect. When analyzed by age group, there seemed to be a developmental trend. The young juveniles had a lower proportion of individuals who used an inverted grip at least once relative to the group of older juveniles. The young juveniles also exhibited a higher frequency of other grips relative to the older juveniles indicating greater variability in the strategies employed to complete the task.

In addition to the first ever demonstration of ESC in this species, three important patterns were highlighted in our results. The first was that there appears to be a developmental trajectory to ESC in vervet monkeys. This was evidenced by the decrease in the use of other grips and the increase in the number of individuals using ESC across all trials from young to older juveniles. The second pattern was the discrepancy between the high proportion of individuals, particularly the older juveniles, using ESC at least once in the context of an overall very low rate of usage. This pattern of findings is not reflected in other nonhuman primate studies examining the ESC effect (e.g., Chapman et al., 2010; Weiss et al., 2007; Zander et al., 2013). Lastly, the third highlighted pattern involved Pilani, the adult female who was missing her right arm and left leg. She used ESC at a higher rate than any of the other monkeys tested. Overall, the findings shed new light on the development of second order planning in nonhuman primates and its relation to the morphological constraint hypothesis (Zander et al., 2013; Rosenbaum et al., 2014).

To the best of our knowledge, there is extremely little published data on the developmental trajectory of second order planning in nonhuman primates. One 4-month-old lemur was found to demonstrate the ESC effect by Chapman and colleagues (2010), but to the best of our knowledge this is the only published evidence of an infant or juvenile nonhuman primate demonstrating ESC. Notwithstanding, the bulk of the developmental data from this task comes from human children. For example, Wunsch and colleagues (2014) used a variant of the cup task originally employed by the original tamarin study (Weiss et al., 2007) in order to create a more direct comparison between children and nonhuman primates. Wunsch and colleagues (2014) found a developmental trajectory in children consistent with other studies (see Wunsch et al., 2016 for a review) and demonstrated that adult humans performed most similarly to the tamarin monkeys. By contrast, in the current study, the young juveniles' performance on the task seemed most comparable to the group of preschool children tested by Wunsch and colleagues (2014). The percentage of young juveniles who demonstrated ESC in at least one of the first 3 trials was 17.6%, arguably comparable to the 22% of preschool children (aged 3.7-6.4 years) showing ESC in at least one trial in Wunsch et al.'s (2014) study.

The use of other grips by young juveniles indicates a higher level of variability in the strategies they implemented to complete the task relative to the older juveniles. 11 out of 17 young juveniles used an other grip at least once in comparison to only 1 out of 6 older juveniles. While the proportion of individuals using other grips is a rudimentary measure for gauging intra-individual variability, it offers suggestive evidence that this variability declines with age in vervets, similar to what is observed in children (Comalli et al., 2016). Decreases in intraindividual variability over development in nonhuman primates could indicate they are testing alternative strategies as part of early learning and are not yet prioritizing the most efficient way to complete the task, again similar to children. While there may be a similar trajectory in juvenile nonhuman primates relative to children, we note the end point of that trajectory for vervet monkeys is still unknown (discussed further below).

The morphological constrain hypothesis postulated that for species with a lack of dexterity and limited grasping postures the costs of not adopting a grasp that accommodates future postures may be greater as they have limited ways to subsequently compensate. Likewise, species with greater manual dexterity may be able to employ numerous strategies in order to compensate for adopting a suboptimal initial grip. With regard to this hypothesis our results provide mixed support. The overall percentage of ESC grips align with the morphological constraint hypothesis because it would be expected that species with higher dexterity would rely less on ESC. Indeed, vervet monkeys use precision grips and appear to have relatively high dexterity, though they are not native tool-users (Harrison & Byrne, 2000; Santos et al., 2006). However, the high proportion of individuals (overall, and in particular the older juveniles) using ESC at least once does not necessarily align with the predictions made by the morphological constraint hypothesis. Rather, this trend tends to emerge in species that are less dexterous and cannot use precision grips. The young juveniles demonstrated ESC in only 10.6% of the first 3 trials, and older juveniles showed it in 11.1% of the first 3 trials. In comparison with other species, capuchins demonstrated ESC in 30% of the initial trials, squirrel monkeys in 90%, tamarins in 83.3% and lemurs in 38% (Chapman et al., 2010; Weiss et al., 2007; Zander et al., 2013). Both the vervet monkeys in this study and the lemurs (Champan et al., 2010) were tested in more naturalistic conditions compared to the more controlled laboratory conditions in which the other species were tested. Chapman and colleagues (2010) postulated that the less controlled conditions could have led to the overall low percentage of ESC even though 10 of the 14 lemurs used ESC at least once. The impact of methodology on the current study might also be leading to lower overall percentages of ESC use. Given these comparisons and the consideration of methodology, it still appears that juvenile vervet monkeys, regardless of age, show ESC less frequently than adults of other primate species when given a similar task. However, a firm conclusion cannot be made due to the potential effect of naturalistic conditions and the potential that adult vervet monkeys would show a higher proportion of ESC more comparable to the adults of other species. Given this result future studies should endeavor to fill in these gaps.

Of all nonhuman primate species given a similar cup-manipulation-task, capuchins are the most similar to vervet monkeys in terms of the ability to use precision grips. The main contrasts between the two species is that capuchins are native tool-users while vervets are not and capuchin hand morphology is quite different than the hand morphology of Old World monkeys. Overall, the proportion of individuals that demonstrated ESC at least once (48%) was comparable to capuchins (40%). However, when these findings are broken down by group, a much larger proportion of older juveniles demonstrated ESC relative to the capuchins. When the vervets were given additional trials, 4 out of 5 of the older juveniles inverted their grip in at least one of those trials while only one of the younger juveniles did so. This also contrasted with findings in capuchins, where none of the individuals given additional trials inverted their grip if they hadn't already done so in the initial trials (Zander et al., 2013). Overall, these results indicated that these two species, which we would expect to look the most similar in response to this task, present with a number of differences. Why these differences occur is still a question that would need to be researched further. Some potential reasons for these differences are differences in dexterity and hand morphology that we are not aware of, the fact that capuchins are native tool-users while vervet monkeys are not, the impact of the comparison of juvenile vervets versus adult capuchins or differences associated with the level of control in the methodology.

The adult female, Pilani, provided an interesting case study for how morphological constraints impact performance on the task. Pilani used ESC at a higher rate than any of the other monkeys tested, 71.4% of her 7 trials. This created an interesting parallel to a condition in the study by Comalli and colleagues (2016) in which they restricted children from using their non-dominant hand in the hammering task by placing an oven mitt over that hand. The result of this manipulation was that their use of ESC increased. Comalli and colleagues (2016) interpreted this result as children having the ability to learn within a single session to avoid an inefficient grip when it was shown to be more costly, which accords with the morphological constraint hypothesis. Pilani used an upright grip (a non ESC grip) in 2 of her 7 trials. In order to be able to adjust her grasp she would most likely have had to put the cup down and then re-grip it, which would not only be inefficient but also potentially costly due to being tested in the enclosure with her cagemates who potentially could have stolen the cup and marshmallow. Thus, it is unclear how Pilani's disability and sharing the enclosure with other monkeys contributed to her greater reliance on ESC.

The other adult monkey tested, Apstert, evidenced a high level of variability in his response to the task. He used an inverted grip in 14.3% of trials, upright in 28.6% and other grasps in 57.1% of his trials. Apstert had epilepsy, and due to this condition, it is possible that he had a level of cognitive impairment that could have impacted his performance in the task. Throughout testing he struggled with the transparent container, often trying to grab or eat the marshmallow through the cup before resorting to picking the cup up. It should be noted that he was the only monkey tested that persisted in showing difficulties with the transparent container during testing.

Unfortunately, the adult data in this study does not lend itself to comparison with adults of other primate species nor give us a good index of how a typical adult vervet might perform on this task. Due to the lack of adult data we cannot know the endpoint of the established developmental trajectory for ESC in vervets. Another limitation of this study arose from the limited amount of time available for data collection. Due to these time constraints, we were forced to prioritize which individuals would receive additional testing trials, leading to inconsistent numbers of trials across individuals. We chose not to test monkeys who had already demonstrated ESC within the first three trials in order to see if those that did not use an inverted grip in the first three trials would with additional exposure. Overall, in this study the vervet monkeys were tested in conditions that were not as controlled as many of the other primate studies into ESC (e.g. Weiss et al., 2007; Zander et al., 2013). Chapman and colleagues (2010) also performed their study with lemurs in a more naturalistic setting comparable to the one in this study and they similarly found low overall percentages of ESC use. The differences in methodology impacted our ability to make firm conclusions when comparing across species.

This study lends itself to future work on second order planning in vervet monkeys and other nonhuman primate species, particularly as it relates to the developmental trajectory of second order planning. In order to understand the endpoint of the developmental trajectory of second order planning and the ESC effect in vervet monkeys, more complete adult data would need to be collected from typical adults. Future studies should also include features that allow more accurate measurements of variability. More nonhuman primates, particularly Old World monkeys, with relatively high dexterity need to be tested in second order planning and ESC studies because the majority of the species tested have been New World monkeys with low relative dexterity.

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ACADEMIC VITA
SARAH R. ANTHONY

EDUCATION

Pennsylvania State University, University Park, PA
College of the Liberal Arts and Schreyer Honors College
Bachelors of Science in Psychology & Biological Anthropology **Class of 2020**
Honors Thesis: The End-State Comfort Effect in Vervet Monkeys (Chlorocebus pygerthrus)

Paterno Fellow and Schreyer Scholar **2017-Present**
Joint venture between the honors and liberal arts colleges including advanced academic coursework, thesis, study abroad and/or internship, ethics study, and leadership/service commitment, in addition to honor's college base requirements.

GRANTS, AWARDS AND HONORS

Dean's List	2015-Present
Nagle Directors Fund Scholarship	2017
Student Engagement Network Grant	2017
Schreyer Honors College Research Grant	2017
Schreyer Honors College Service Grant	2017
Schreyer Honors College Research Grant	2019
Liberal Arts Enrichment Funds – Susan Welch Dean's Chair Scholarship	2019

RESEARCH INTERESTS

Social cognition and behavior in non-human primates. Broadly, I am interested in the evolution and development of cognition and behavior in the primate lineage.

RESEARCH EXPERIENCE

Research Assistant **Aug. 2017 – Present**
Penn State Language and Cognition Lab, College of Liberal Arts, Pennsylvania State University

- Ran participants through various experiments conducted by the lab related to language and motor planning
- Was a data manager on a multi-site project, which entailed reliability coding, updating remaining tasks, securing personal data, and prepping video data for open access
- Attended weekly lab meetings
- Presented at a lab meeting on my honors thesis research and planning for that experience

Volunteer Research Assistant **Feb. 2019 –May 2019**
Bambelela Wildlife Care and Vervet Monkey Rehabilitation Center, Limpopo Province, South Africa

- Collected data for my honors thesis research with juvenile and adult vervet monkeys
- Secured necessary IACUC

- Primary caretaker of the “Handicap Cage” which houses sanctuary monkeys that are unable to be released
- Helped the medical team by handling monkeys while injuries are bandaged and administering medicine
- Experience was fully funded by the Schreyer Honors College and the College of Liberal Arts at Penn State

Research Assistant **Jun. 2017 – Jul. 2017**

Field Projects International, Madre De Dios, Peru

- Collected behavioral data on multiple groups of Emperor and Saddleback Tamarins
- Participated in full day follows collecting focal and scan data and running playback experiments related to vocal communication
- Organized and coded the behavioral data that was collected

Research Assistant **Jan. 2016 – Aug. 2016**

Project SIESTA (Study of Infants' Emergent Sleep TrAjectories), College of Health and Human Development, Pennsylvania State University

- Main responsibly included coding video data of infant sleep routines
- The project studies patterns infant sleep and the relationship with parent-infant functioning during the day
- Project funded by the National Institute of Child Health and Human Development and is under the direction of Dr. Douglas Teti

WORK AND VOLUNTEER EXPERIENCE

Building Supervisor **Aug. 2017 – Dec. 2018**

Penn State Campus Recreation, University Park, PA

- Assisted with supervision of Campus Recreation facilities. Perform all work in cooperation with professional staff in accordance with department policies and procedures
- Assisted with direct supervision of facility attendants, communicating all pertinent information and delegating tasks to facility attendants
- CPR, First Aid and AED Certified
- Provided exceptional customer service
- Ensured facilities are safe and secure

Long-Term Volunteer and Monkey Caretaker **Oct. 2014 – Apr. 2015**

Bambelela Wildlife Care and Vervet Monkey Rehabilitation, Limpopo Province, South Africa

- Primary caretaker for the “Kindergarten Cage” which houses the juvenile monkeys aged 5 months – 3 years and three adult females
- Responsibilities included cleaning, feeding, observation, and assuring the well-being of the monkeys
- Experience catching and handling vervet monkeys for medical procedures, etc.
- Involved with three troop releases