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A Foray into the Interval Timing Capabilities of Tufted Capuchin Monkeys (*Cebus [Sapajus] apella*)

by

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A Proposal Submitted to the Honors Council
For Honors in Animal Behavior

5/20/2021

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Abstract

Time is a critical part of life and timing on the range from milliseconds to minutes has proven to be critical for several behaviors such as foraging and movement. While the exact neurological structures of interval timing are currently undefined, several studies have been completed comparing the interval timing capabilities of humans and nonhuman primates. However, these studies have unanimously utilized members of *Macaca*, which limits the abilities for researchers to make apt comparisons between humans and all nonhuman primates. This study sought to investigate whether tufted capuchins (*Cebus [Sapajus] apella*) have the capability to measure time on the interval level (interval timing) and can demonstrate this in response to visual stimuli. The subjects of this experiment, while showing low error and high overall performance, did not display any knowledge of the interval length as indicated by the distribution and time of touches. Further experimentation utilizing stricter punishment and higher rewards alongside an extended experimentation time may provide results more in line with the hypothesis of this study.

Keywords: internal time measurement, timing production tasks, accuracy, time perception, comparative cognition, human-primate comparisons

Introduction

There are various systems for measuring time over different magnitudes (Helm et al., 2017). The most familiar of these is circadian timing, which is responsible for behaviors over the course of a day, such as appetite and the sleep cycle (Buhusi & Meck, 2005). In contrast, the ability to time short periods from the seconds-to-minutes is called interval timing (IT; Buhusi & Meck, 2005; Buhusi et al., 2006). IT has been identified in many vertebrate species, including birds, fish, rodents, human, and nonhuman primates (NHPs; Bateson, 2003; Buhusi & Meck, 2000; Buhusi & Meck, 2005; Buhusi, et al. 2006; Cabeza de Vaca et al., 1994; Jozefowicz et al., 2005; Kleinman et al., 2016; Matell & Meck, 1999; Ohyama et al., 1999; Sherburne et al., 1998). In animals, measuring time in the span of microseconds is important for using echolocation, while measuring time in the milliseconds to seconds range is involved in motion processing (Ivry, 1996; Merchant & de Lafuente, 2014). A bulk of IT research has been related to foraging, especially in connection to the optimal foraging theory (OFT) (Bateson, 2003; Bateson & Kacelnik, 1997; Brodbeck, Hampton, & Cheng, 1998; Buhusi & Meck, 2005; Buhusi et al., 2006; Cerutti & Staddon, 2004; Daan & Koene, 1981; Gill, 1988; Kacelnik & Brunner, 2002; Mayo and Sommer, 2013).

How time is measured in the brain varies with the scale of time being measured – for example, the suprachiasmatic nucleus of the hypothalamus has been implicated in measuring circadian time (Buhusi & Meck, 2005). Theories on the neural underpinnings of the internal measurement of IT have varied over the years; one of the first explanations

was the pacemaker-accumulator model, which dictates that a dopaminergic pacemaker sends regular pulses and that these pulses are temporarily stored in an accumulator (Buhusi & Meck, 2005; Gallistel & Gibbon, 2000). A later modification of the pacemaker-accumulator model is the scalar expectancy theory, which also posits that IT is marked by an internal clock, but that clock is also associated with memory and decision-making (Brodbeck et al., 1998; Staddon, 2005; Staddon & Higa, 1999). An alternative to the pacemaker-accumulator model, Behavioral Theory of Timing, instead relies on operant and classical conditioning; the pacemaker instead relies on the rate of reinforcement, increasing or decreasing in response to the interreinforcer interval (García-Garibay et al., 2016; Lejeune et al., 2006; Killeen & Fettermen, 1988). The cognitive processes for measuring time in the interval range remains an active topic of study for neurologists interested in the measurement of time.

While the exact mechanisms for IT measurement are currently unclear, IT has still been widely researched in different species, with a notable amount of research comparing the IT capabilities and mechanisms of NHPs and humans (Cabeza de Vaca et al., 1994; García-Garibay et al., 2016; Merritt et al., 2010; Oneo et al., 2011; Zarco et al., 2009). IT is important in movement for humans and NHPs, and in speech for humans (Zarco et al., 2009). Previous studies working with timing have focused on rhythm entrainment to visual and auditory tempos (García-Garibay et al., 2016; Merchant & Honing, 2014; Takeya et al., 2017), temporal and spatial categorization (Mendez et al., 2011; Merritt et al., 2010), and interval production (Kleinman et al., 2016; Zarco et al., 2009). This research in total has so far found that while NHPs showed a similar ability to humans to

internally follow visuo-spatial rhythms of various tempos (without overt movements; García-Garibay et al., 2016), NHPs did not fare as well as humans with timing using auditory stimuli (Zarco et al., 2009). Further research into the IT capabilities of NHPs, especially as they compare to human capabilities, can prove essential to providing insight on how IT develops as an ability and how these variations within a related group are influenced by ecological and behavioral factors.

Most subjects chosen for these comparative IT experiments are macaque monkeys (*Macaca spp.*), a cercopithecoid genus widely used in animal research and testing (Zarco et al., 2009). This singular use of macaques as a test subject in comparison to humans limits the validity of broad comparative statements to all NHPs, as *Macaca* is not a representative for other NHPs. Since we currently do not know how IT is measured within the brain, we do not know how broad differences will be between species, even those that are closely related. The current differences between humans and macaques indicate that there are at least significant differences in the internal mechanisms of IT measurement across genera, as NHPs were less capable IT with auditory stimuli. This is especially important to consider, as studies detailing neurological models for timing treat macaques as a stand-in for all NHPs (Leon & Shadlen, 2003; Mendez et al., 2011; Merchant & Bartolo, 2018; Merchant et al., 2013, 2015; Merchant & Honing, 2014; Onoe et al., 2001).

Platyrrhine NHPs (commonly called New World monkeys) have been studied on similar cognitive topics as their catarrhine (Old World monkeys) relatives, but the capabilities and mechanisms of IT in platyrrhine NHPs has not been thoroughly

investigated. One platyrrhine genus well known for their cognitive abilities is the capuchin monkey (*Cebus spp.*). Like with other primates, IT is essential for capuchins due to its connection with movement and communication, as well as foraging (Bateson, 2003; Ivry, 1996; Merchant & de Lafuente, 2014). Research in topics adjacent to IT – such as memory over delay, episodic memory, and delayed matching-to-sample paradigm – indicate that capuchins perform well in these cognitive tasks (D’Amato & Worsham, 1972; Janson, 2016; Judge et al., 2005). But as of the writing of this paper, no studies have been conducted looking at IT in capuchins, or any other member of the platyrrhine parvorder. The present study seeks to fill that void in IT research by studying the extent of IT capabilities in platyrrhine species. The present study focused on whether brown capuchins (*Cebus [Sapajus] apella*) have the capability for interval timing by internalizing the length of a stable time interval.

Methods

Subjects and Housing

Subjects are four adult captive-born brown capuchin monkeys – three females and one male. All subjects are housed in a mixed-sex social colony of 17 individuals located at Bucknell University in Lewisburg, PA, USA. All subjects were tested in their home enclosure, which is made up of three connected rooms divided into compartments (a full description of the enclosure is described by Lutz and Judge (2017)). The temperature of the enclosure is between 75-79° Fahrenheit and the humidity is between 47-53%. The enclosure has a light-dark cycle of 12h:12h with light onset at 6:30am. Subjects are fed

twice a day, with a diet of monkey chow (commercial primate diet produced by Mazuri Primate Browse Biscuits), nuts, legumes, and vegetables. Monkey chow and water are available ad libitum throughout their enclosure.

Materials

Visual stimuli were chosen for this study because of previous work indicating that NHPs were more accurate at IT with visual stimuli than auditory stimuli (Merchant & Honing, 2014; Zarco et al., 2009). To deliver these stimuli, subjects were presented with a computerized testing apparatus that consists of an 1590L 15" Open Frame Touchscreen mounted to a metal frame attached to a rolling cart. This monitor was connected to a Dell laptop running Presentation (version 20.1). This screen displayed different images according to each subjects' progress in the experiment.

Procedure

Subjects were tested individually within a compartment, being physically blocked off from other subjects and members of the group for the duration of the session. During the testing session, the subjects were given physical access to the touch screen. At the start of a trial, the screen displayed a black screen with a small green square on the lower center (Figure 1). All subjects have had prior experience and training with touchscreens and the layout of this start screen, removing the necessity for training before this experiment. After initiating the trial by touching the start square, the stimulus – a large red square in the center of the screen– was displayed for 4000 milliseconds on a black background (Figure 1). This 4000ms period in which the sample stimulus was displayed but during which touches were not counted is hereby known as the *sample*

display period. Touches to the screen or stimulus during this time were recorded but did not advance or abort the trial. After the sample display period was completed, the *touch period* began, which lasted for 5000 milliseconds. The first touch to the red square during the touch period resulted in positive reinforcement, with subjects being given 1 sunflower seed for each successful completion of a trial as well as a positive auditory stimulus. A trial error or failure is when a subject failed to touch the square during the 5000ms touch period, in which case the screen returns to the trial initiation phase without reinforcement as well as a negative auditory stimulus. At the end of each trial, the screen automatically returned to the trial initiation phase, allowing the subject to initiate and complete another trial. Each session consisted of 20 trials. At the end of each session, the subjects were rewarded with five sunflower seeds for the completion of a session regardless of proficiency throughout the session.

Training Phase. There were four stages in the training phase, each with increasing background darkness (Figure 1). Stage 1 is a light gray, almost white color, while Stage 4 is practically indistinguishable from the black background of the sample display period. The intent of these stages of training is to provide the subject with a visual cue for the start of the touch period, to train them that touches are only registered after the 4000ms sample display period. As the subject advances through the training stage, the decreased brightness of the background changes at the touch period encourages them to rely less on the background color change as a cue for the end of the sample display period, and instead on their internal processes for timing to indicate when to touch the screen during the touch period. A subject was considered proficient in a stage if they successfully

completed 19 out of 20 trials within a session, in which they were advanced onto the next stage upon the next session.

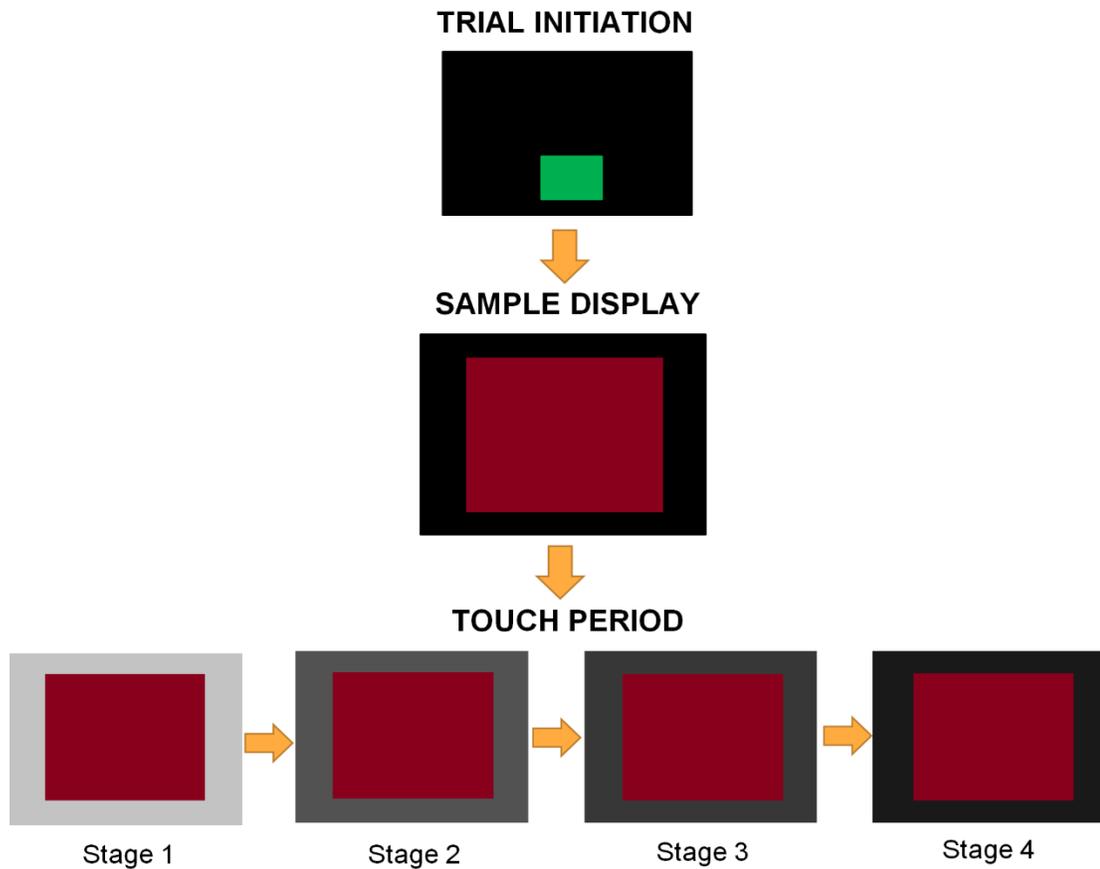


Figure 1. Diagram showing the screens as displayed to the subjects during the training phase.

Testing Phase. Upon proficiency of Stage 4, the subjects were moved onto the testing phase. The testing phase consisted of five sessions in which the touch period of this phase was visually identical to Stage 4 of the training phase: a red square upon a

black background. Proficiency was scored but did not factor into whether a subject could progress.

Data Collection

The results of each trial were recorded in Presentation through the Dell laptop, with an individual file for each subject. The files contained data from each session including the subject's name, the date and time of the session, the session number, the trial number, the phase (training or testing), the stage (1 – 4, during the training phase), the success of each trial, the given reward, the response latency during the touch period, and the timestamps of all touches made during the sample period. The results of each trial for both phases were also noted by hand.

Data Analysis

The data were analyzed utilizing Excel via the Data Analysis ToolPak. Analyses focused on three separate touch behaviors, 1) the number of touches in the sample display period, 2) the temporal distribution of touches during the sample display period, and 3) the latency to first touch during the touch period. These variables were chosen because they indicate whether the subjects had learned the interval length – if they had, the number of touches would be low or nonexistent in the sample display period, the distribution of any touches in the sample display period would be close to the end of the period, and the first touch during the touch period would be close to the beginning. These variables were calculated for each subject for each of the 4 training phases and in the testing phase. To determine if subjects changed their responding over the course of training and testing, two separate repeated measures ANOVAs were performed; one on

the number of touches during the sample period across the phases, and one on the latency to first touch during the touch period across the phases. Learning rate across the phases was assessed by examining each subject's errors to criterion for each stage in the training phase. Performance in the 100-trial testing phase was calculated for each subject as the proportion of trials correct.

Results

On average the subjects took 12 sessions to complete the entire training phase, with most of these sessions spent on the first and second stages (Table 1). The percentage of errors made during the training phase remained below 25%, indicating that in general, subjects moved through the training phases without many errors (Figure 2).

Subject Name	Number of Sessions Completed	Number of Trials Completed	Sessions to Completion			
			Stage 1	Stage 2	Stage 3	Stage 4
Deangela	13	259	7	6	1	1
Niko	13	259	2	6	4	1
Nye	9	179	4	3	1	1
Schroder	13	259	11	1	1	1
Average	12	239	6	4	1.75	1

Table 1. Completion data for the training phases.

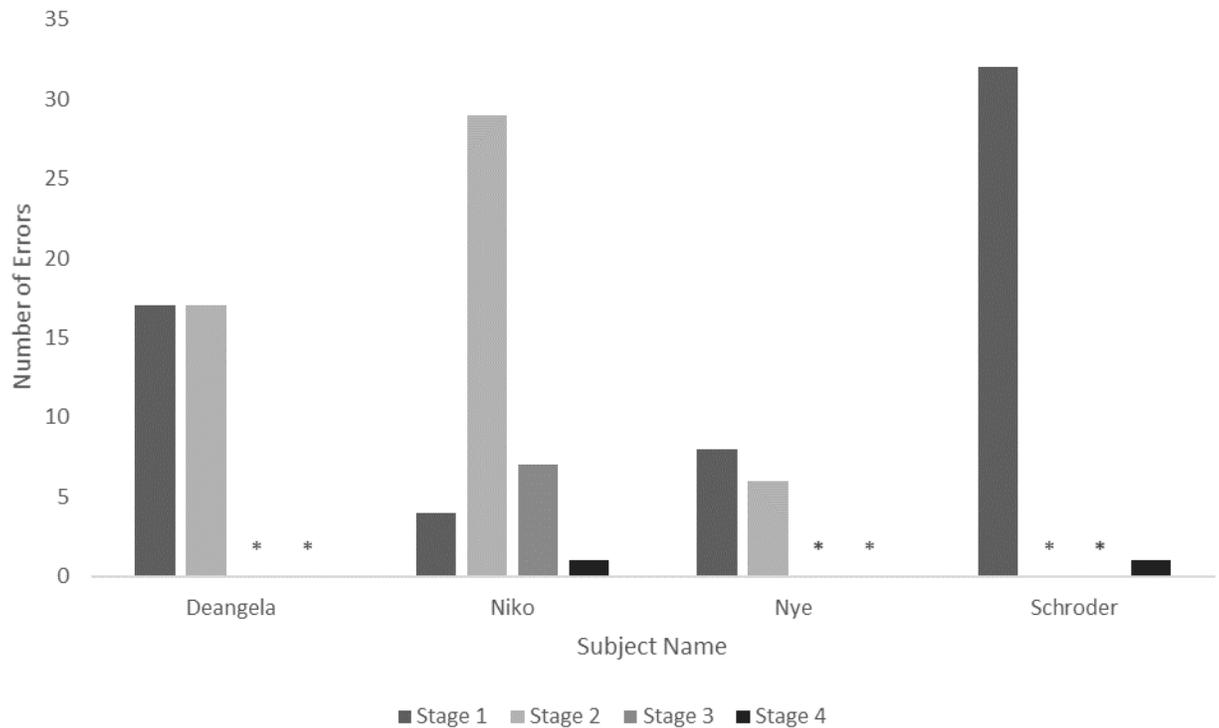


Figure 2. Number of errors for all subjects during the training phase. The asterisks indicate that no errors were made.

Touch Period Latency

While a repeated measures ANOVA revealed a significant main effect of stage on touch period latency in the training and testing phases ($F(4,12) = 3.67, p = 0.036$), there was not a systematic decrease in the average latencies of the first touch across stages for most subjects, as would be expected if the subjects learned the duration of the interval. The exception is Deangela, who saw a steady decrease in average touch period latency

across phases (Figure 3).

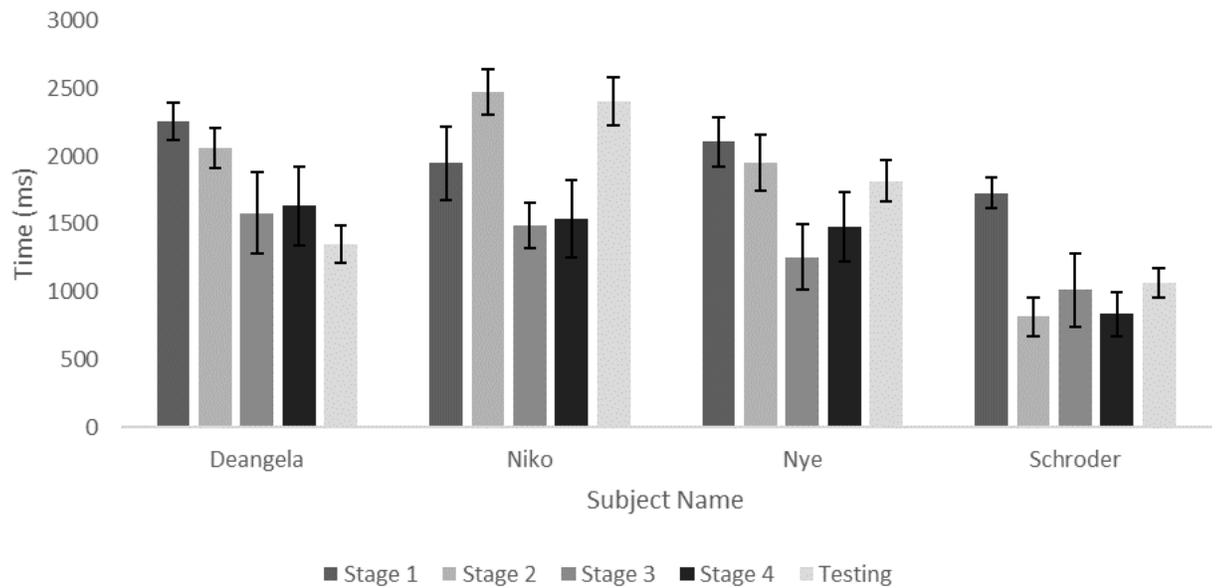


Figure 3. Latency to interact with the screen during the touch period across each stage of the training phase and all sessions of the testing phase for each subject.

Number of Touches

The average number of touches during the touch period showed a slight non-significant decrease over the training phase but remained between 2 to 3 touches per trial ($F(4, 12) = 0.70, p = 0.606$; Figure 4). An outlier was Nye, who had an average of 4.95 touches during Stage 4, but 2.45 touches during the testing phase.

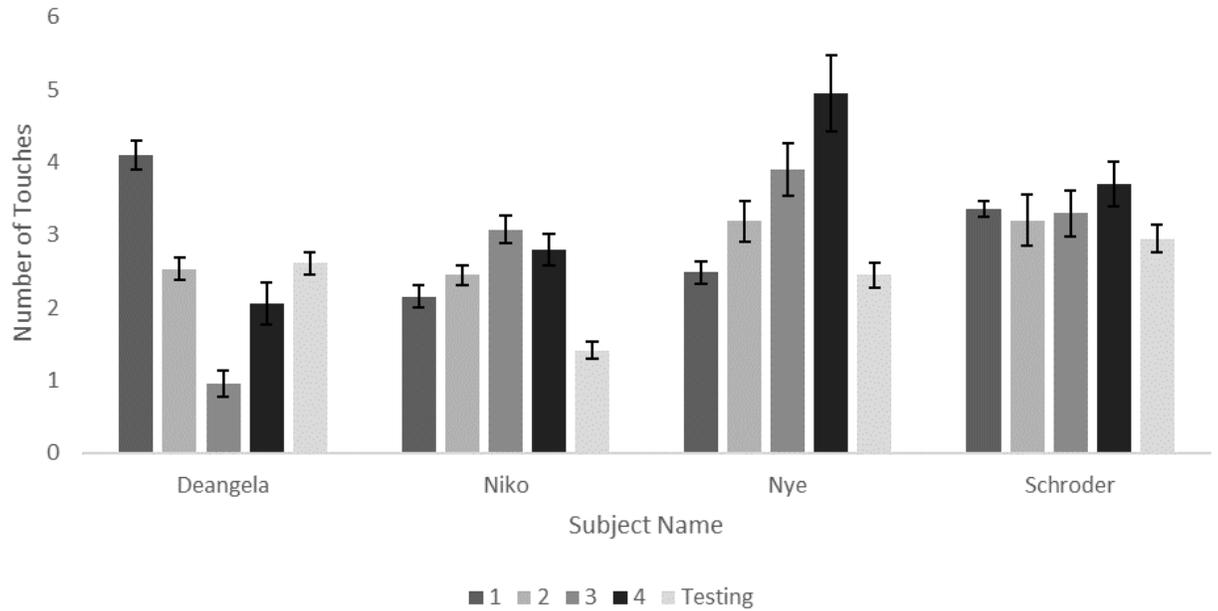


Figure 4. Average number of touches across each stage of the training phase and all sessions of the testing phase for each subject.

Performance

The average performance for the testing phase was $90\% \pm 28.84\%$. Niko had a performance of $79\% \pm 40.73\%$, the lowest of all subjects, while Schroder had the highest performance at $96\% \pm 19.60\%$ (Figure 5).

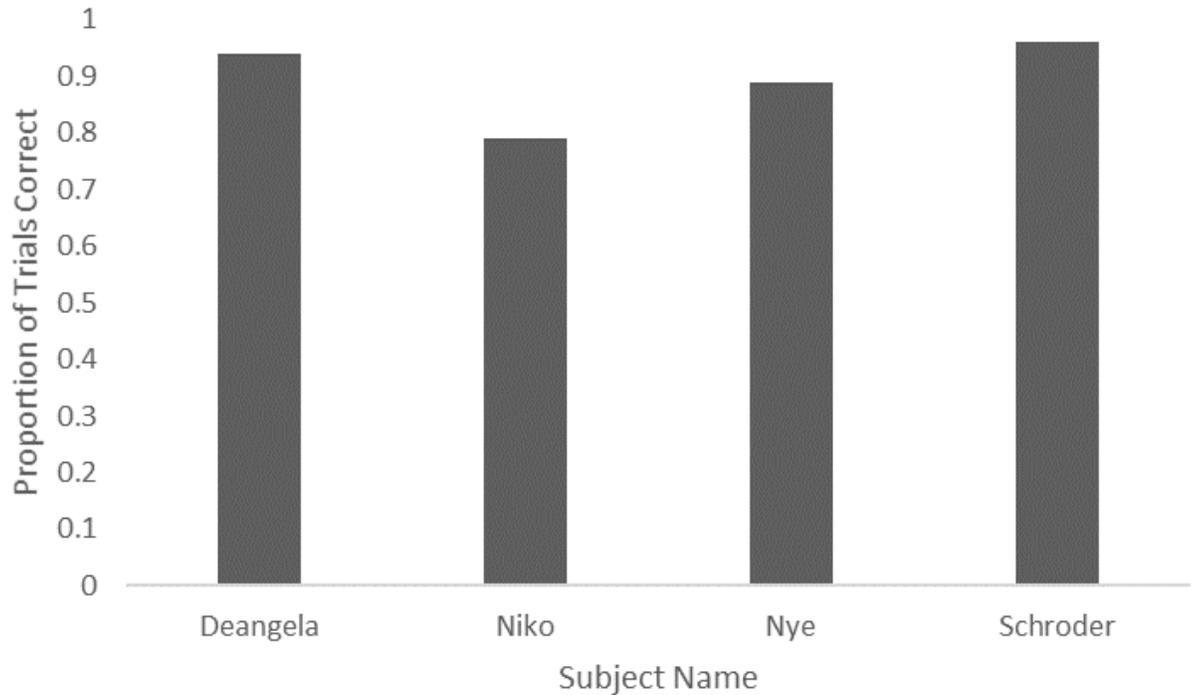


Figure 5. Overall performance in the testing phase for each subject.

Sample Display Interactions

The overall distribution of the first touches made by each subject were not centered around 4000 milliseconds, which would be expected if they learned the length of the sample display interval. Instead, the subjects' first touches in the testing phase were clustered around 1000 to 2000 milliseconds (Figure 6), with an average touch time of 1427.16 milliseconds (Figure 7).

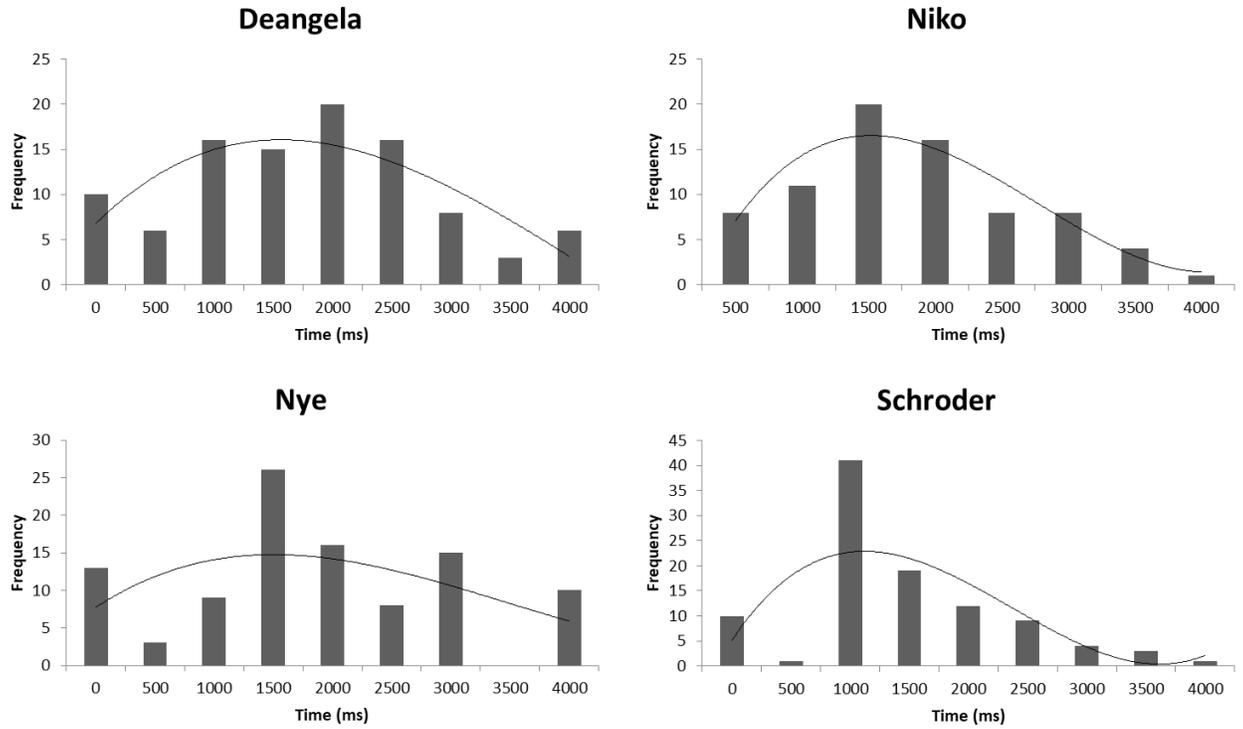


Figure 6. Individual histograms for the distribution of touches made during the sample display period of the testing phase. A subject that had learned to wait until after the sample period to touch would show a distribution skewed towards 4000 ms.

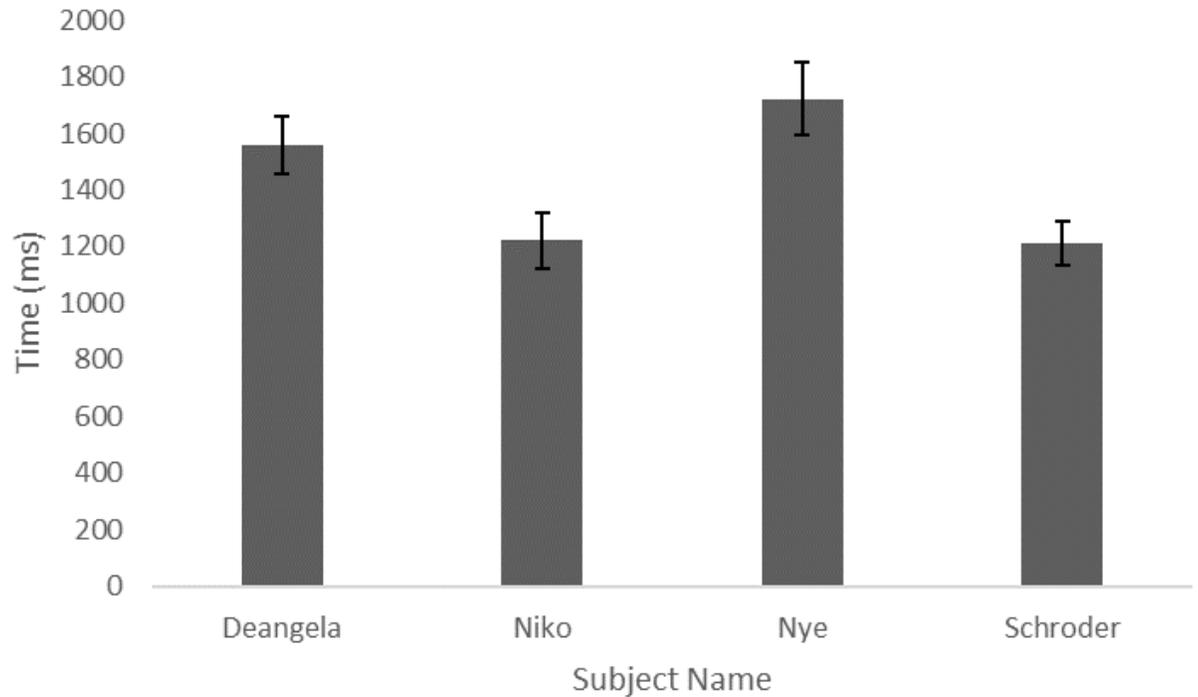


Figure 7. Average latency to the first touch during the sample display period for each subject in the testing phase. Error bars indicate standard error of the mean.

Discussion

While subjects showed low errors to criterion in the training phase and high performance in the testing phase, analysis of touch latency during the sample display and interaction period during the training and testing phases, as well as the overall number of touches, indicates that the subjects' touch patterns were not consistent with use of IT. If the subjects internalized the sample interval length, their first and subsequent touches on the screen during the sample display period should have been distributed around 4000 milliseconds, with the average across the subjects showing a similar range. Instead, the subjects' touch distribution centered around 1000 to 1500 milliseconds, with the average being around 1000 to 2000 milliseconds. Similarly, the subjects' latency to interact with

the screen during the touch period should have been close to immediate – around 500 to 1000 milliseconds. But this was not seen in the results; most of the subjects interacted with the screen at between 1000 and 2000 milliseconds. Further, there should be few touches during the sample display period and at least one touch registered during the touch period. Instead, subjects touched the screen two or more times throughout all phases of the experiment, garnering up to five touches on average.

These results imply that the subjects did not learn the interval length and were merely touching the screen until a reward was given at the end of the trial. There are a few factors in the methods of this experiment that may have contributed to these results.

Lack of Punishment and Level of Reinforcement

The subjects were neither punished nor rewarded for touching during the sample latency period, meaning that if they did learn the sample display interval, they had no incentive to show this knowledge through changes in the frequency or timing of their touches; this is known as latent learning (Chamizo & Mackintosh, 1989; Williams, 1995). Several nonhuman primates have been observed purposefully displaying performance patterns that were not consistent with their knowledge, including tufted capuchins (Drea & Wallen, 1999; Mitchell & Anderson, 1997). The only punishment given to the subjects in this experiment was during the touch period, in which subjects were negatively punished for not touching the screen within 5 seconds. This also meant that impulsivity in the form of rapid touching would not be discouraged during the sample display period.

Previous work on monkeys on interval timing, time awareness, and interval comparison have utilized negative punishment to train their subjects on interval tasks, as

well as increasing the level of reward a subject received for performing with higher accuracy or lower error to criterion (Mendez et al., 2011; Zarco et al., 2009). Tufted capuchins have shown risk aversive behaviors in the past, meaning that negative punishment could be effective in correcting touching patterns (Chen et al., 2006; De Petrillo et al., 2015; Venticelli et al., 2013). Similarly, changing the level of reward for higher accuracy performance can also be effective as perceived reward value of reinforcement has been shown to have an impact on tufted capuchins' performance in cognitive tasks (Gazes et al., 2018). Therefore, such methods may have been necessary for the subjects to display any knowledge they gained through the course of this experiment.

Number of Trials

The methodology of previous studies on timing in nonhuman primates differed drastically from the procedures of this study in the overall number of trials, their frequency, and training procedures. For example, the rhesus macaques in Zarco et al. (2009) performed their interval tasks for on average four hours a day – around 1,000 trials – almost every day of the week. The data obtained for the García-Garibay et al. (2016) study consisted of 47,235 total trials from 358 sessions over the course of four months, following 10 months of training. In our study, our subjects completed an average of 339 trials, testing 2 – 4 times a week over the course of 17 months. The comparatively short period for data collection and training, and the lengthy periods of inactivity due to scheduling challenges in the present study no doubt limited how much the subjects could learn and retain. While the monkeys in the present study did progress through the training

phases, it is entirely possible that more time was needed to internalize the knowledge of the interval, as they could very well have learned a tactile response to the task rather than internalizing a set length of time.

Subject Movement and Bystander Interference

This experiment did not utilize primate chairs, which have been used in previous timing experiments to fixate the heads of primate subjects (Kleinman, Sohn, & Lee, 2016; Mendez et al., 2011; Zarco et al., 2009). The subjects, while limited to one compartment during the session, were still able to move freely away from the screen at any time. Not only were the subjects freely allowed to move, but the subjects also had both auditory and visual access to their social group, which despite the subjects' general attentiveness during a session, could and did interfere with their performance, which has been documented in tufted capuchins and other nonhuman primates (Beran et al., 2012; Coyne, 2010; Drea & Wallen, 1999; Mitchell & Anderson, 1997).

Suggestions for the Future

Future attempts at studying IT in capuchin monkeys can take on a variety of modifications, including but not limited to increasing the total number of trials a subject completes, increasing the reward for touching at the right time, and punishing subjects for touching at the wrong time. All of these would be done with the purpose of increasing the efficacy of the experiment by encouraging the subjects to learn and display their memory and capacity for internal timing.

Regardless of the methods used to do so, continuing this research is imperative to the study of IT in nonhuman animals as well as understanding the cognitive abilities of

nonhuman primates, particularly those of the platyrrhine parvorder. As IT has been related to movement, foraging, and vocalizations (in humans particularly), expanding the research on IT to more members of the primate family can also provide insight into the development of these abilities in humans and nonhuman primates alike (Bateson, 2003; Bateson & Kacelnik, 1997; Buhusi & Meck, 2005; Buhusi et al., 2006; Mayo and Sommer, 2013; Merchant & de Lafuente, 2014; Zarco et al., 2009).

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