Reach-to-Grasp Kinematic Signatures in Colombian Spider Monkeys
(*Ateles fusciceps rufiventris*)

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A defining feature of most primates is a hand with five fingers. Spider monkeys are an exception because they have four fingers and no thumb. Despite the prevalence of reach-to-grasp research in primates, it is not known how the lack of a thumb affects reaching and grasping in spider monkeys. Drawing on patterns that have been well described in human adults, human infants, and other nonhuman primates, this study characterized prehension in Colombian spider monkeys (*Ateles fusciceps rufiventris*). Monkeys reached for two differently sized food objects and reaches were digitized offline for two-dimensional kinematic analysis. Grasp strategy was coded from video as preshaped when the hand was adjusted to grasp the food before contact, or not preshaped when the hand was adjusted to grasp the food after contact. Monkeys exhibited variability in reach smoothness that contrasted with the typical pattern seen in other adult primates and instead resembled the pattern observed in human infants. Monkeys anticipated the object to be grasped approximately half of the time. Reaches where the hand was preshaped to the object were smoother than reaches where the hand was adjusted to grasp after object contact. For the small object, reaches with preshaping were straighter than reaches without preshaping. Results are the first evidence of kinematic signatures for reach-to-grasp actions in spider monkeys.

Keywords: reaching, grasping, kinematics, spider monkey, platyrrhine

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A hand with five digits—synonymous with reaching and grasping in primates—does not describe spider monkeys. Spider monkeys have four digits on their hand and no thumb. Thus, they lack the characteristic opposability that primates are known for, and their anatomy has been regarded as a rate limiter with regard to how the hands are used (Fragaszy, 1998; Heffner & Masterton, 1975; Torigoe, 1985). In our prior work with Colombian spider monkeys (*Ateles fusciceps rufiventris*), we noticed variability in hand orientation while grasping a raisin during reaching trials collected for a handedness assessment (Nelson et al., 2015). On some trials, the hand seemed to curve in advance of contact with the raisin, while on other trials, the hand appeared to be adjusted *after* contact had been made. However, grasp strategy was not analyzed in that project. These informal observations motivated the main research question in the current study: how does the lack of a thumb impact spider monkey prehension? To answer this question, we used a comparative framework to gauge spider monkeys' reach-to-grasp actions against established benchmarks in humans and other nonhuman primates.

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Prehension Patterns in Humans

In this section, we define prehension, provide key benchmarks in human adults, and describe how these patterns differ in infants because this literature guided our hypotheses and predictions. Prehension is traditionally defined as two components: an initial reaching phase to transport the hand to an object followed by a second grasping phase where the hand opens and closes on the object (Jeannerod, 1981, 1984). There is an extensive literature examining the structure of human reaching and grasping using two-dimensional (2-D) or three-dimensional (3-D) kinematic assessment (for a review, see Egmose & Koppe, 2018).

There are three notable aspects of how the hand moves through time and space in human adults, and these patterns are robust to variation in experimental tasks (e.g., Engdahl & Gates, 2019; Flash & Hogan, 1985). First, reaches have a distinctive shape in the hand speed profile resembling a bell curve from a single acceleration followed by a single deceleration (onespeed peak). This property of reaching has been described as *smoothness*. Adult reaches are very smooth. Second, adult reaches are *straight*, which is determined by the ratio of the path the hand traveled against the straight-line distance between where the hand started and the target. Third, there is a speed-accuracy tradeoff in adult reaching (Fitts, 1954). Reach speed decreases when greater accuracy is required like for precision grips.

Studies with infants have shown reach kinematics differ across development (Berthier & Keen, 2006; Bhat & Galloway, 2006; Corbetta & Thelen, 1996, 1999; Fetters & Todd, 1987; Konczak & Dichgans, 1997; Konczak et al., 1995; Mathew & Cook, 1990; Ronnqvist & Domellöf, 2006; von Hofsten, 1979). Relative to adult reaches, infant reaches tend to have multiple hand speed peaks, indicating movements are less smooth. In addition, straightness ratios in infants are larger, indicating immature movements that are less straight as compared to adult movements. Finally, the speed of infant reaching decreases with age (Berthier, 2011).

Like reaching, grasping has a distinctive signature in adults that differs from infants. Adult grasping involves preshaping the fingers to the target before the hand makes contact (Jeannerod, 1999). A popular metric for quantifying preshaping is maximum grip aperture (MGA), which is a measurement of the widest opening between the thumb and forefinger where smaller MGAs indicate greater precision. Visually, there is a peak in MGA that reliably follows the peak in hand speed (Paulignan et al., 1990). Critically, reach kinematics differ as a function of the grasp (power or precision grip) that will be used (Gentilucci et al., 1991), suggesting that reaching and grasping are integrated to some extent under normal conditions (for a discussion, see Rouse et al., 2019). Without visual guidance, however, reaching and grasping in adults become sequential: the hand is open during reaching and touches the target before haptic cues guide the hand to close in a grasp (Karl & Whishaw, 2014; Karl et al., 2012).

Young infants, new to reaching, haptically react to objects like unsighted adults and there is a gradual shift in their ability to integrate visual information about the target such that the wrist is oriented to the object in anticipation and there are refinements when the hand opens and closes for grasping (Barrett et al., 2008; Fagard, 2000; Karl & Whishaw, 2014; Lockman et al., 1984; McCarty et al., 2001; Morrongiello & Rocca, 1989; Newell et al., 1989; Piéraut-Le Bonniec, 1985; von Hofsten & Fazel-Zandy, 1984; von Hofsten & Rönnqvist, 1988; Wentworth et al., 2000; Witherington, 2005). The emergence of preshaping in infants, measured initially by some developmental researchers as *anticipatory hand orientation* and later using the metric MGA like adults, is very protracted. Levels of preshaping do not yet resemble adults by 2 years of age (Karl & Whishaw, 2014).

Taken together, there are marked differences in reaching and grasping benchmarks between human adults and infants. In the current study, we tested our main hypothesis that reach parameters (smoothness, straightness, and average speed) differ as a function of grasp strategy (preshaped grasp vs. no preshaped grasp) in spider monkeys. For spider monkey reaches with preshaping, we predicted patterns resembling adult benchmarks (including adult primates of other species; see "Prehension Patterns in Nonhuman Primates" section). Alternatively, spider monkey reaches without preshaping were predicted to resemble human infant patterns. We next turn to prehension patterns in nonhuman primates before outlining the current study.

Prehension Patterns in Nonhuman Primates

Prehension is the most widely studied function of the hands in nonhuman primates (Fragaszy & Crast, 2016), however, research examining reach-to-grasp behavior from 2-D or 3-D kinematics has largely focused on macaques (for a review, see Castiello & Dadda, 2019). These studies have predominantly measured reaching and grasping in adult monkeys against the benchmarks for adult humans described in the prior section (but see Nelson et al., 2012). From this body of work, we know that macaque monkeys share several features of reaching and grasping with human adults. Relevant to the current study, macaques show a single peak bell-shaped hand velocity profile and scale their grip aperture to the object to be grasped (Christel & Billard, 2002; Mason et al., 2004; Rouse & Schieber, 2015; Roy et al., 2000, 2002, 2006; Sartori et al., 2013b, 2014; Scott & Kalaska, 1997). Like human adults, macaques similarly adjust reach speed to object size by reaching faster to larger objects (Roy et al., 2002) and the kinematics of the reach vary depending on how an object will be grasped (Rouse & Schieber, 2015; Sartori et al., 2013b).

A much smaller literature has examined reach-to-grasp kinematics in nonhuman primate species besides macaques, and no study has reported on spider monkeys. We are also unaware of any reach-to-grasp studies in colobus monkeys, who like spider monkeys, do not have a thumb. Colobus monkeys are catarrhines (formerly "Old World" monkeys) like macaques, whereas spider monkeys are platyrrhines (formerly "New World" monkeys).[1] Given the paucity of research, Table 1 compares all prior reach-to-grasp kinematic publications on platyrrhine monkeys relative to the current study and the hypotheses that were tested.

Like macaques, some findings from platyrrhine studies that have examined reach-to-grasp kinematics resemble human adult benchmarks, while others hint at some differences or leave questions unanswered. Work by Reghem and colleagues identified that adult capuchins (as well as adult ring-tailed lemurs, adult gorillas, and adult chimpanzees) show the classic bell-shaped velocity profile associated with smooth reaches in human adults (Reghem et al., 2013). Fox et al. (2019) reported that the timing of the velocity peak and MGA in marmosets was like other adult primates including

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[1] New World and Old World are dated terms stemming from colonialism. The recommended labels for these taxonomic groups are platyrrhine and catarrhine monkeys, respectively.

Table 1

Kinematic Studies Examining Reach-to-Grasp Actions in Platyrrhine Monkeys Including the Number of Individuals Studied, Species, Type of Kinematic Analysis and Setting, and Whether the Effects of Grasp Type or Object Size on Reach Kinematics Were Analyzed

Source	N	Species	Type of kinematic analysis and setting	Reach × Grasp	Reach × Object size
Current study	3	*A. f. rufiventris*	2-D post hoc Zoological Park Constrained	Yes	Yes
Fox et al. (2019)	2[a]	*C. jacchus*	3-D post hoc Laboratory Constrained	No	No
Mundinano et al. (2018)	4[a]	*C. jacchus*	2-D post hoc Laboratory Constrained	No	No
Takemi et al. (2014)	6[a]	*C. jacchus*	3-D real-time Laboratory Constrained	No	No
Fragaszy (1983)	14	*S. sciureus*	3-D post hoc Laboratory Unconstrained	No	Yes
Reghem et al. (2013)	3	*S. xanthosternos*	3-D post hoc Zoological Park Unconstrained	No	No

Note. Platyrrhine is an inclusive term that replaces the colonial term New World monkeys. N = number of subjects.
[a] Number of control animals only. Type of kinematic analysis and setting for data collection: 2-D = two-dimensional, 3-D = three-dimensional, post hoc = kinematic data extracted from video frame-by-frame, real-time = kinematic data collected from reflective markers worn by monkeys, constrained = monkey reached through aperture, unconstrained = no restrictions on limb movements. Reach × Grasp: the authors reported analyzing kinematic data as a function of grasp type (yes/no), Reach × Object Size: the authors reported analyzing kinematic data as a function of object size (yes/no).

humans. Fox et al. (2019) additionally reported that marmosets were unable to scale their grip to object size, which is relevant for the current study because marmosets have a nonopposable thumb but share the same digital dexterity rating as spider monkeys (Heffner & Masterton, 1975). In fact, no platyrrhine studies have examined whether reach kinematics vary as a function of grasp because investigators working with these models have reported on power grips exclusively as a single grasp category. Although investigators have varied object size in experiments with platyrrhines, only Fragaszy (1983) reported on the relation between reach kinematics and object properties, finding that general prehension patterns in squirrel monkeys did not differ by object or object size grouping. Moreover, Fragaszy (1983) was the only investigator to provide straightness ratios in any platyrrhine study on reach-to-grasp kinematics, finding that values for squirrel monkeys were higher than those typically observed in human adults but lower than what has been reported in human infants (for a richer discussion of the human literature, see Berthier & Keen, 2006).

To summarize prehension patterns in nonhuman primates, there is evidence in support of our main hypothesis that reach kinematics vary as a function of grasp in macaque monkeys, but this hypothesis has not been tested in any platyrrhine monkey species. When reach smoothness has been examined, adults in all nonhuman primate models to date show the single speed peak characteristic of human adults. Nonhuman primate studies typically have not reported on reach straightness, and findings relating average reach speed to object size vary by species. The current study addresses these knowledge gaps relative to human prehension patterns by measuring reach smoothness, straightness, average speed, and grasp strategy using video-based motion tracking of reach-to-grasp actions in spider monkeys.

Current Study

The purpose of the current study was to characterize prehension in spider monkeys by examining reach-to-grasp kinematics for the first time using comparative benchmarks. This work extends the call from Fragaszy and Crast (2016) for a shared taxonomy to evaluate manual functions in primates. Based on a review of human and nonhuman primate literature, we hypothesized that reach kinematics vary as a function of grasp. Anecdotal observations suggested that spider monkeys may use anticipatory hand postures, albeit not exclusively. Thus, we expected two types of grasps: one in which the hand is preshaped to the target and another without any preshaping. We predicted when monkeys preshaped the hand to the target, reaches would resemble adult human/macaque benchmarks (i.e., smoother, straighter, and slower speed due to greater accuracy needed), whereas reaches with no preshaping would resemble human infant benchmarks (i.e., less smooth, less straight, and faster speed).

In addition to our main hypothesis of kinematic signatures by grasp, we also examined whether object size influences reach-to-grasp kinematics in spider monkeys. In general, object size affects grasp selection in primates—smaller objects tend to elicit a switch to a precision grip (e.g., Elliott & Connolly, 1984; Pouydebat et al., 2009). We used small- and large-sized food pieces in our reach-to-grasp experiment and predicted that reaches to the large object would be smoother, straighter, and faster relative to reaches to the small object because of the motor demand associated with grasping small objects, which may be exacerbated without a thumb. Finally, we tested for grasp strategy by object size interactions on reach-to-grasp kinematics. Spider monkeys were videotaped with a high-speed camera reaching to cereal (small object) or grapes (large object), and 2-D kinematic analysis was performed post hoc.

Method

Openness and Transparency

We report how we determined our sample size, all data exclusions, all manipulations, and all measures in the study. Processed data, R code, and output are publicly available at the following link: https://osf.io/8dznf/ (Nelson et al., 2023).

Subjects

Data were collected from three Colombian spider monkeys (*A. f. rufiventris*) housed at the wildlife park Monkey Jungle in Miami, Florida, USA. The sample consisted of one male and two females ranging in age from 4 to 8 years old. All subjects were captive-born and mother-reared. However, the social group also included an additional adult female who participated in the study given the design (see "Procedure" subsection) but was excluded from analysis due to rearing history. Food and water were freely available throughout the study. Monkeys were fed commercial chow (Purina LabDiet 5045, USA) and a mix of fresh fruits and vegetables by park staff twice a day. Monkeys were also fed dried fruit and seeds from tourists visiting the park. During data collection, monkeys had full access to an outdoor main enclosure measuring 8.84 m × 3.96 m × 4.47 m as well as an adjoining indoor night house measuring 3.30 m × 1.09 m × 2.72 m. All housing areas were equipped with vertical and horizontal structures. Rotating enrichment toys were available during the study. All monkeys had previous experience participating in hand and/or tail laterality studies but were naïve to the experimental procedure used to collect reach-to-grasp data for kinematic analysis.

Procedure

Pilot observations indicated that monkeys frequently used their mouth to pick up food from indoor perches in their enclosure. To induce manual responses, a testing platform (43.18 cm × 43.18 cm) was set up outside of the monkeys' indoor night house at the height of one of the perches to create a testing surface equivalent to ground level. Vertical cage bars in the monkeys' enclosure effectively constrained monkeys to use their hands only. The spacing between bars offered some leeway for the monkey's arm to move left to right, and greater flexibility for the arm to move top to bottom. A Basler A640 monochrome camcorder was positioned on a tripod at the level of the testing platform to record the monkeys' responses at 100 Hz within MaxTRAQ 2D software (Innovision Systems Inc., Columbiaville, Michigan). The camera was positioned perpendicular to the 2-D reaching plane and provided a left-side view of the monkeys' movements (see Figure 1 and the online supplemental material).

Three experimenters participated in data collection (Eliza L. Nelson, Megan A. Taylor, and Armando del Valle). A trial consisted of Experimenter 1 (Megan A. Taylor) presenting either a whole grape (large object: ∼3.00 cm) or a Froot Loops™ cereal (small object: ∼1.27 cm) to the focal subject's midline within arm's reach and recording the reach-to-grasp response. The foods selected for the experiment were based on dietary preferences in the group. A trial began when a single monkey sat in front of the testing platform and the trial ended when the food was consumed. Presentation order was pseudorandomized in blocks of four trials so that the same size object was not presented more than twice consecutively. Experimenter 2

Figure 1

Schematic of the Experimental Testing Setup
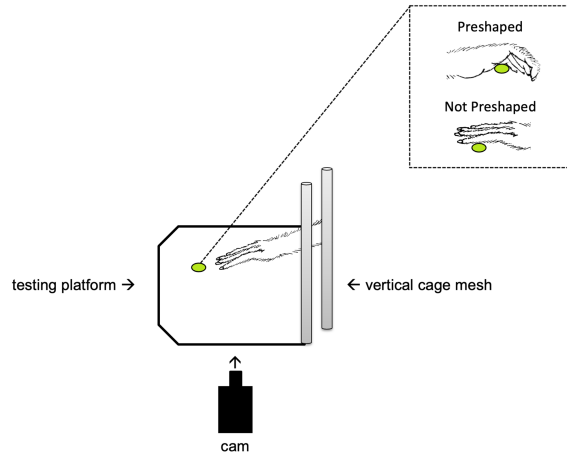
Note. Spider monkeys reached through vertical cage mesh for a single object placed on a testing platform outside of their enclosure. A camera recorded a left-side view of monkeys' movements. The callout box shows spider monkey grasp strategies illustrated from the side view. In the preshaped grasp, the digits are flexed, and the hand is preoriented to the object at target contact. By comparison, the digits are extended in an exploratory posture and the hand is flat at target contact when grasp was not preshaped. See the online article for the color version of this figure.

(Armando del Valle) announced the run order aloud and recorded which monkey responded on each trial in a paper log. Subject testing order was random, as monkeys could choose whether to participate in the reach-to-grasp task throughout each session. No monkey was separated from the group for the experiment. Experimenter 3 (Eliza L. Nelson) operated a trigger switch to record each trial to a laptop that was connected to the camera and coordinated the synchronization with Experimenter 1 and Experimenter 2.

Data were collected over three nonconsecutive 1.5-hr sessions from March to June 2018. The number of trials varied by monkey and session. The Institutional Animal Care and Use Committees of Florida International University (Protocol #16-047) and the DuMond Conservancy (Protocol #2012-03) approved the procedure, and the work was carried out in accordance with the laws of the United States. The research adhered to the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates. Monkey Jungle staff monitored monkeys' welfare during data collection.

Behavioral Analysis

Hand Preference Calculation

The experimental task required a manual response; however, monkeys could choose which hand to use on each trial. To determine if monkeys exhibited hand preferences under the testing constraints, a handedness index (HI) was calculated from the first 90 successful reaches per monkey (cf., Nelson et al., 2015) by subtracting the number of left hand reaches from the number of right hand reaches and then dividing by total, $HI = (R - L)/(R + L)$. HI scores range from

−1.00 (exclusive left hand reaches) to 1.00 (exclusive right hand reaches). Individual preferences were determined by binomial z scores, where $z < -1.96$ = left preference, $z > 1.96$ = right preference, and all other z scores = no preference. Z score cutoffs correspond to $p < .05$ for two-tailed tests.

Grasp Strategy Coding

The grasp strategy for picking up the food target was scored from video based on the orientation of the hand and degree of digit flexion at target contact as preshaped or not preshaped (Figure 1 box). A grasp was coded as preshaped when there was evidence of preshaping the hand to the target before contact through digit flexion and rotating the hand up to 90° to be perpendicular to the testing surface. No preshaping was coded when two operational criteria were met: no digit flexion and the hand was parallel to the testing surface. Put another way, the hand was flat with extended digits in a neutral exploratory position upon contact with the food and then adjusted to the object for the grasp strategy without preshaping. Two experimenters (Armando del Valle and Narciso Pavon) independently coded grasp strategy from video recordings. Interrater reliability was calculated on 10% of all successful reaches recorded using the formula: (Total − Disagreements)/Total. Grasp reliability was 93%. Disagreements between coders for grasp strategy coding were resolved through discussion.

Kinematic Analysis

Kinematic data were analyzed from 20 trials for each monkey. To standardize comparisons, we selected trials where the focal monkey was seated with one hand stationary on the cage mesh prior to the start of the trial. Additional inclusion criteria included that the food was stationary prior to the start of the reaching response, and that the focal monkey consumed the food at the end of the trial. Since no markers could be placed on the monkeys, reaches were manually digitized offline using the software program MaxTRAQ 2D (Innovision Systems, Inc., Columbiaville, MI; see the online supplemental material). A single point on the radial wrist was chosen as a landmark because it could be consistently identified across frames and remained stable throughout the duration of the reach. Reach onset was operationally defined as the first frame of arm movement toward the food. Reach offset was defined as the first frame of hand contact with the food. The coordinate system was scaled using the known length of the testing platform that was always visible during filming. Post hoc analysis was consistent with prior studies in nonhuman primates (Nelson et al., 2012; Reghem et al., 2014; Sartori et al., 2013a).

2D kinematic data were extracted and processed with Matlab (The MathWorks, Inc., Natick, MA) using custom programs. Data were low-pass filtered at a frequency of 6 Hz with a second-order dual-pass Butterworth filter. A three-point difference formula was used to calculate speed (mm/s) because only position is recorded from the wrist marker, not velocity, so velocity must be estimated from the position data. A three-point difference formula is a standard numerical way to calculate velocity from three recorded position points by averaging the distance traveled over three points and dividing it by the data recording frequency. Average speed was the mean speed of the frames during the reach. Reach duration was calculated as the time in seconds between the reach onset and the reach offset.

Straight-line distance was calculated as an estimated straight-line between the starting position of the wrist marker and the ending position of the wrist marker. Path length was calculated from the length of the actual path the wrist marker traveled. Reach straightness was computed by the ratio of wrist path length to straight-line distance. Values closer to 1 indicate straighter reaches (Churchill et al., 2000). Reach smoothness was computed as movement units using an algorithm derived from von Hofsten (1991). Here, a movement unit was defined as a significant acceleration (a difference from the peak of the preceding valley of 20 mm/s and having an average acceleration of 50 mm/s during the rise from the preceding valley to the peak) followed by a similarly sized deceleration. Visually, one movement unit resembles a bell curve in the wrist-speed profile. Movement unit values closer to 1 indicate smoother reaches.

Statistical Analysis

All analyses were conducted in R Version 4.1.0 (R Core Team, 2021). Linear mixed-effects models were used to examine the effect of monkeys' grasp strategy (preshaped or not preshaped) and object size (large or small) on the dependent reaching variables of smoothness, straightness, and average speed using the R package *lme4* (Bates et al., 2015). Duration and straight-line distance were used as covariates to control for differences in arm length where appropriate in models. Outliers were defined as values 2.5 times the interquartile range and were excluded from analyses. Based on these criteria, one data point was excluded in the model examining reach smoothness. In order to provide p values for tests of fixed effects, degrees of freedom for t tests were approximated with Satterthwaite's method using the R package *lmerTest* (Kuznetsova et al., 2017). α was .05.

Results

Monkeys Have Robust Individual Hand Preferences

All monkeys exhibited significant hand preferences at the individual level on the reach-to-grasp task. Individual hand-use data, HI scores, and z scores are given in Table 2. Two monkeys were right-handed, and one monkey was left-handed. One monkey made two reaches with the nondominant hand in the trials that were digitized for kinematic analysis. All other monkeys used their dominant hand exclusively. Thus, hand effects (i.e., left vs. right, preferred vs. nonpreferred) on spider monkey reach-to-grasp kinematics were not examined.

Monkeys Preshaped Grasp Half of the Time

Grasp strategy was coded from the 60 trials used in kinematic analyses (see Figure 1 box and Figure S1 in the online supplemental material). There were 30 reaches to the large object and 30 reaches to the small object. As a group, monkeys used the preshaped grasp strategy on 32 trials and did not preshape on 28 trials. Table 2 shows the distribution of grasp strategies used by object size for individual monkeys. On average, monkeys preshaped approximately half of the time ($M \pm SD = 53.33 \pm 7.64\%$). Wilcoxon signed ranks tests found that grasp strategy was unrelated to object size (all $ps > .05$). Monkeys were equally likely to preshape or not preshape, and there was no preferred grasp strategy for reaching to cereal pieces or grapes.

Table 2
Individual Hand Preference Data and Distribution of Trials Used in Kinematic Analysis by Grasp Strategy and Object Size

| | | | Hand preference | | | | Object size | | |
ID	Age	Sex	L/R	HI	z	Grasp strategy	Large	Small	Total
Cary	5	F	0/90	1.00	+9.38	Preshaped	5	4	9
						Not preshaped	3	8	11
Jeni	4	F	89/1	−0.98	−9.17	Preshaped	6	5	11
						Not preshaped	5	4	9
Mason	8	M	1/89	0.98	+9.17	Preshaped	7	5	12
						Not preshaped	4	4	8
Total							30	30	60

Note. Sex: F = female, M = male. Hand preference: L = number of left hand reaches, R = number of right hand reaches, HI = handedness index, z = binomial z score. HI was calculated with the following formula: HI = (R − L)/(R + L). Significance was determined by binomial z scores, where $z < −1.96$ = left preference, $z > +1.96$ = right preference, and all other z scores = no hand preference.

Monkeys' Reaches Have Multiple Speed Peaks But Were Smoother With Preshaping

Table 3 shows the means and standard errors for all reach parameters as a function of grasp strategy and object size, and Table 4 shows the estimates of the model regression coefficients, 95% confidence intervals of those coefficients, and *p* values. Reach smoothness was measured by the number of movement units, or speed peaks in the wrist profile. Only 20% of reach-to-grasp actions resembled the typical adult primate profile of a single movement unit, or one acceleration followed by one deceleration. The modal number of movement units for spider monkeys was two, and 40% of reach-to-grasp actions contained three or more movement units (Figure 2A). There was a significant effect of grasp strategy on reach smoothness (Figure 2B). Reaches coupled with the preshaped grasp strategy were smoother than reaches paired with no preshaping. Reach smoothness did not vary as function of object size, and the interaction between grasp strategy and object size on reach smoothness was not significant. All monkeys exhibited variability in reach smoothness as measured by max number of movement units. For two monkeys, the max number of movement units was five and for one monkey the max number of movement units was four. An example of a reach with one movement unit (the minimum for all monkeys) is shown in Figure 2C. A reach with two movement units (the modal group pattern) from the same monkey is shown for comparison in Figure 2D.

Monkeys Made Straighter Reaches to Small Objects With Preshaping

There was a main effect of object size on reach straightness (Tables 3 and 4). Reaches to the larger object were straighter than reaches to the small object. There was also a significant interaction between grasp strategy and object size (Figure 3). Reaches to small objects, but not large objects, differed in straightness as a function of grasp strategy. Reaches to the small object where the monkey used the preshaped grasp strategy were straighter than reaches to the small object where no preshaping was used. There was no main effect of grasp strategy on reach straightness.

Monkeys' Average Speed Did Not Differ by Grasp Strategy or Object Size

There were no effects of grasp strategy, object size, or interactions between grasp strategy and object size on reach average speed (Tables 3 and 4).

Discussion

The main goal of the current study was to characterize prehension in spider monkeys by examining reach-to-grasp kinematics for the first time relative to comparative benchmarks in humans and nonhuman primates. We tested two hypotheses for kinematic signatures in spider monkeys: (a) reach kinematics differ as a function of grasp strategy and (b) reach kinematics differ as a function of object size. Monkeys reached for a small (cereal) or large (grape) object under constrained conditions to induce manual grasping and reaches were digitized post hoc for 2-D kinematic analysis. In some trials, monkeys preshaped their hand to the object, whereas in other trials monkeys did not preshape, but rather contacted the object with a flat hand and then adjusted grasp. Hypotheses were partially supported, suggesting specific reach-to-grasp kinematic signatures in spider monkeys.

Table 3
Means and Standard Error for Reach Parameters as a Function of Grasp Strategy and Object Size

| | Grasp strategy | | Object size | |
Reach parameter	Preshaped	Not preshaped	Large	Small
Smoothness[a]	2.13 ± 0.16*	2.64 ± 0.23*	2.41 ± 0.20	2.33 ± 0.20
Straightness[b]	1.12 ± 0.02	1.18 ± 0.03	1.12 ± 0.02**	1.17 ± 0.02**
Average speed	510.94 ± 30.38	458.32 ± 28.58	485.29 ± 35.94	487.48 ± 22.76

[a] Measured by number of movement units. Values closer to 1 indicate smoother reaches.   [b] Measured by ratio of hand path length to straight-line distance. Values closer to 1 indicate straighter reaches. Unit for speed is mm/s.
* *p* < .05.   ** *p* < .01.

Table 4

Estimates of the Model Regression Coefficients, 95% Confidence Interval of Those Coefficients, and p *Values*

Reach parameter	b	95% CI	p
Smoothness			
Grasp strategy	0.55	[0.04, 1.07]	.04*
Object size	0.17	[−0.35, 0.69]	.53
Grasp strategy × Object size	−0.19	[−1.23, 0.85]	.72
Straightness			
Grasp strategy	0.02	[−0.43, 0.48]	.28
Object size	−0.06	[−0.11, −0.02]	.01**
Grasp strategy × Object size	−0.10	[−0.19, −0.01]	.03*
Average speed			
Grasp strategy	−51.77	[−123.86, 20.32]	.17
Object size	7.96	[−64.64, 80.55]	.83
Grasp strategy × Object size	−55.10	[−200.22, 90.02]	.46

Note. CI = confidence interval.
* $p < .05$. ** $p < .01$.

Reaching and Grasping May Be Partially Synchronized in Spider Monkeys

Results from the current study confirmed our anecdotal observations—spider monkeys use a mix of preshaped and not preshaped grasping strategies when reaching for food. As a group monkeys anticipated grasp on half of the trials, and preshaping the hand was not systematically tied to either of the food sizes used in the study. Individually, monkeys preshaped the hand to the object on 45%–60% of reaches. Preshaping was unrelated to grasping success, as monkeys obtained the food in all trials. Soppelsa et al. (2022) examined preshaping in another nontraditional reaching and grasping model without a thumb, African savannah elephants, reporting that half of their sample shaped the trunk tip to the object type and the other half showed no preshaping. Like spider monkeys, preshaping was not tied to elephants' grasping success. These findings suggest individual differences in scaling an effector to an object, which mirrors patterns observed in human infants. Corbetta et al. (2000) found that a subset of 5- to 9-month-old infants consistently scaled their hands to objects of different sizes. Another subset of infants scaled their hands inconsistently when object size was varied, and a final subset did not scale their response to object size at all. These patterns contrast with observations of adult humans and adult macaques who reliably preshape their hand to the object to be grasped (e.g., Jeannerod, 1999; Roy et al., 2000).

When monkeys did not preshape, the hand was adjusted after contacting the object, indicating that the grasp strategy may be haptically guided. However, monkeys were very accurate in transporting the arm to the target; they did not touch the testing platform first and then search for the food like young human infants, but rather fixed the arm in place to grasp (I. Whishaw, personal communication). Using the framework from Karl and Whishaw (2014), reaching and grasping seem to be partially synchronized in spider monkeys since preshaping was not the predominant grasping strategy used. It is unknown what conditions, if any, would increase preshaping rate in spider monkeys. In tufted capuchins, Christel and Fragaszy (2000) found preshaping increased when the dexterity demands of the task increased. Alternatively, increasing task demands may lead spider monkeys to grasp food with another body part such as

their mouth, foot, or tail (Nelson & Kendall, 2018). Determining whether there is any ecological advantage for manual preshaping in spider monkeys requires further investigation.

We did not record a frontal view of the monkeys' movements, so we cannot say with confidence if or when spider monkeys' actions were visually informed. This question requires scoring what the eyes are doing throughout the reach in our future work. Neurotypical human adults visually fixate on a food target just before starting to reach and blink or look elsewhere after grasping (de Bruin et al., 2008). Whishaw et al. (2016) reported that a rhesus monkey (Helen) with a primary visual cortex (V1) lesion also visually fixated on a food target and blinked when the hand contacted the food. This behavior is notable because Helen reached with an open hand and only formed a grasp after touching the food, like what we reported in some of our spider monkey trials where we observed no preshaping. Moreover, children and adults with cortical lesions also show open hand reaching and difficulties in grasp formation in the affected hand, particularly in conditions with no vision (Jeannerod, 1986). Congenitally blind adults do scale their hand to an object but open and close the hand twice relative to once as in sighted adults, suggesting that visual experience rather than the experience of vision itself may be responsible for differences in reach-to-grasp patterns (Castiello, Bennett, & Mucignat, 1993). Examining the coupling between eye movements and hand movements in future experiments will allow us to further interpret reach-to-grasp patterns in spider monkeys.

Preshaping Has Kinematic Signatures in Spider Monkeys

Predictions for how grasp strategy would affect reach kinematics in spider monkeys were partially supported: reaches with preshaping were smoother, but not slower, than reaches without preshaping. Although some reaches did have the classic single peak velocity profile observed in other primates (and human adults), it was not the typical pattern for spider monkeys. The modal number of movement units (i.e., the metric for smoothness) was two and the maximum was five. In this regard, spider monkey reaches broadly resembled human infant reaches with multiple speed peaks. Relative to human benchmarks, monkeys' reaches were smoother when an adult-like grasping strategy (preshaping) was used versus an infant-like grasping strategy (no preshaping). Multiple accelerations and decelerations in wrist speed over the course of a reach have been interpreted in the human infant literature as a sequence of corrected submovements (Berthier, 2011). Submovements may be indicative of the difficulty of a movement task (Meyer et al., 1988). Model simulation has revealed further insights into the processes underlying kinematic patterns in human reaching behavior. Schöner et al. (2018) approximated the differences between human infant and adult reaches by simulating impairments in three areas: movement planning, movement timing, and motor control. They found that reaches were less smooth (aka more movement units) and no longer straight. Simulation may be an interesting avenue for disentangling differences observed in spider monkeys reaching relative to patterns in humans and other primates in future research.

The relation between reach straightness and grasp strategy was more complex. In general, straightness ratios in spider monkeys approached floor levels ($M = 1.1$), indicating that reaches were fairly straight as seen in human adults (e.g., Nelson et al., 2018; $M = 1.1$) as well as infant rhesus monkeys (Nelson et al., 2012; $M = 1.1$). Reaching was unconstrained in both the adult human and infant

Figure 2
Reach Smoothness for Reach-to-Grasp Actions in Spider Monkeys Is Variable
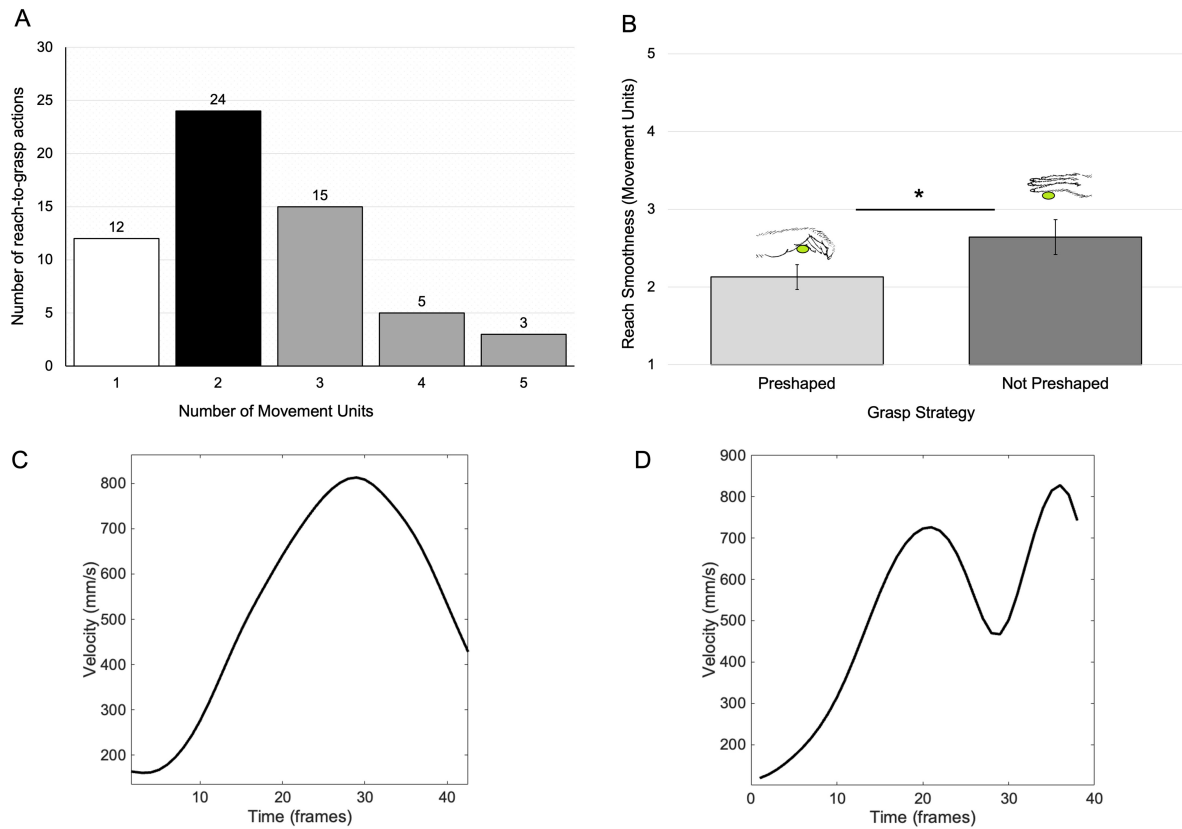
Note. The graph in (A) shows how reach smoothness, measured as the number of movement units, was distributed across reach-to-eat actions in all monkeys. The open bar denotes the typical reach smoothness pattern in primates, including adult humans (one movement unit). The black bar denotes the modal number of movement units for spider monkeys (two movement units). The gray bars denote three or more movement units, which resemble patterns observed in human infants. The graph in (B) shows a significant effect of grasp strategy on reach smoothness. Reaches with preshaping were smoother than reaches without preshaping. The graphs in (C) and (D) illustrate examples of reach-to-grasp actions from the same monkey (Cary). One movement unit is shown in (C) from a reach to the large object with preshaping. Two movement units are shown in (D) from a reach to the small object without preshaping. See the online article for the color version of this figure.
* *p* < .05.

rhesus monkey studies. Thus, we caution that we cannot rule out that the physical constraints imposed by the spider monkeys' vertical cage bars in the current study could have contributed to these similarities. By comparison, straightness ratios have been reported to be higher (i.e., reaches less straight) in adult squirrel monkeys (Fragaszy, 1983; *M* = 1.3–1.45) with the highest values in human infants (∼2 at reach onset; for a discussion, see Berthier & Keen, 2006). Returning to spider monkeys, reaches to the smaller of the two objects tested (i.e., Froot Loops™ cereal) differed in straightness by grasp strategy. When monkeys reached to the cereal piece and the grasp was preshaped, reaches were straighter. This interaction, coupled with the effect seen in reach smoothness, confirms there are specific kinematic signatures associated with preshaping in spider monkeys, despite the finding that preshaping is not spider monkeys' predominant grasping strategy.

Object Size Plays a Role in Reach Kinematics in Spider Monkeys

Predictions for how grasp strategy would affect reach kinematics in spider monkeys were partially supported: reaches to the larger object (grape) were straighter, but not smoother or faster, than reaches to the smaller object (cereal). This finding of straighter reaches to large objects versus small objects is consistent with human adult literature (Churchill et al., 2000), but differs from the variability seen in human infant literature. For example, Rocha et al. (2006) reported that reaches to a large object were smoother, but not straighter or faster, in 4- to 6-month-old infants. Carrico and Berthier (2008) found reaches to a large object were smoother and faster, but not straighter, in 15-month-old infants. In the closest nonhuman primate study, Fragaszy (1983) found no effects of object size on reach

Figure 3

Grasp Strategy by Object Size Interaction on Reach Straightness
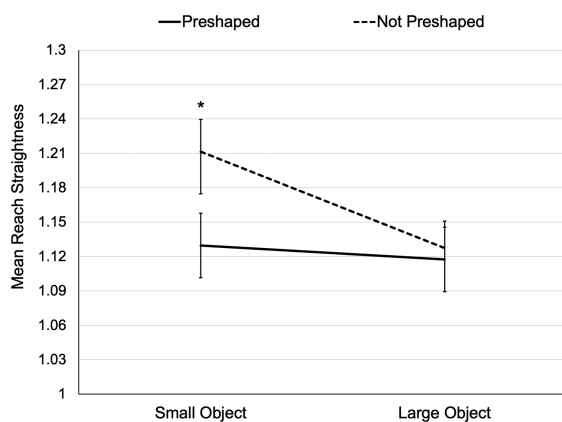
Note. There was a difference in straightness for reaches to small objects as a function of grasp strategy such that reaches with preshaping were straighter than reaches without preshaping. There was no difference in straightness for reaches to large objects between the two grasp strategies. Straightness was computed by the ratio of hand path length to straight-line distance (see text for details).

* $p < .05$.

kinematics in squirrel monkeys. Moreover, size is only one object property that may affect reaching and grasping. For example, grasping has been shown to be influenced by food consistency in strepsirrhines (Peckre et al., 2019). In most grasping studies, including this one, object size has been confounded with object consistency. In the current study, the smaller item (cereal) was hard whereas the larger item (grape) was soft. By rigorously exploring object properties, not only would we be able to tease apart reach-to-grasp comparisons across species, but we would also be able to create a comprehensive grasp catalog for spider monkeys, like prior work in other nonhuman primate species (e.g., Byrne et al., 2001; Christel, 1993; Gérard et al., 2022; Jones-Engel & Bard, 1996; Macfarlane & Graziano, 2009; Marzke & Wullstein, 1996; Pouydebat et al., 2009, 2011; Spinozzi et al., 2004; Truppa et al., 2016). Taken together, we see further characterizing the different grasps used by spider monkeys as a key research target for advancing our understanding of how the lack of a thumb impacts reach-to-grasp actions.

The virtues of the primate thumb and its opposability have been widely discussed for tasks involving manipulation, but surprisingly few studies have considered the contribution of the thumb in reach-to-grasp tasks in humans. Drawing on a case study of a 13-year-old girl, Wing and Fraser (1983) suggested that the thumb may serve as a spatial reference for guiding the transport component of reaching, finding that the position of the thumb is stable, whereas the index finger moves to close the grip aperture in advance of object contact for a precision grasp. This pattern of thumb invariance during reach-to-grasp movements was confirmed in a study of human adults by Galea et al. (2001), who additionally found that the extent of index finger movement corresponded to object orientation. Tracking individual fingers during the reach with motion analysis (cf. Castiello, Bennett, & Stelmach, 1993) may provide additional insight into how the digits are recruited for preshaping in spider

monkeys in the absence of the thumb. It is also important to investigate which part of the hand contacts the object and how the digits move to close grasp, both with and without preshaping. There is variability in digit contact strategies for a precision grasp even among human adults, who reliably preshape (Wong & Whishaw, 2004), and variability in human infants who complete most of the grasp after object contact (Karl et al., 2019). In other words, which digit(s) contact the object and which digit(s) move to close grasp are not the same within and across individuals. The current study did not capture digit movement. Examining where objects of different sizes, weights, shapes, and orientations contact the spider monkey hand, and how the hand closes to form the grasp without the thumb will further reach-to-grasp comparisons across primates.

Limitations and Future Directions

One limitation of this study was that prehension was only examined when monkeys were seated and under constrained conditions. While this approach is consistent with much of the work in this field, how the hands are used in reaching has been shown to be sensitive to posture in nonhuman primates (for a discussion, see Nelson, 2022). Reghem et al. (2014) compared prehension patterns for sitting versus a quadrupedal posture in gorillas and human adults and reported no effect of posture. However, Sartori et al. (2014) replicated kinematic signatures in macaques in a seated posture, but not tripedal (i.e., reaching after walking). Additional experiments could examine reach-to-grasp kinematics in unconstrained conditions that are ecologically valid for spider monkeys such as horizontal clinging or tail suspension.

Conclusions

The current study provides the first evidence of kinematic signatures for reach-to-grasp actions in spider monkeys. When monkeys preshaped their grasp to the object, reaches were smoother overall and reaches to the small object only were straighter. Although preshaping was not the predominant grasping strategy in spider monkeys, these findings suggest that spider monkeys, despite lacking a thumb, are capable of sophisticated reaching and grasping. These findings challenge historical notions of the limits of the spider monkey hand and move the field closer to a shared taxonomy for evaluating manual functions in primates.

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