

RESEARCH ARTICLE

Control of Movement

String-pulling by the common marmoset

 Mathilde Bertrand,^{1,2*} Michael Karkuszewski,^{2*} Rhonda Kersten,^{1,2}  Jean-Jacques Orban de Xivry,^{3,4} and  J. Andrew Pruszynski^{1,2}

¹Department of Physiology and Pharmacology, Western University, London, Ontario, Canada; ²Western Institute of Neuroscience, Western University, London, Ontario, Canada; ³Department of Movement Sciences, KU Leuven, Leuven, Belgium; and ⁴Leuven Brain Institute, KU Leuven, Leuven, Belgium

Abstract

Coordinated hand movements used to grasp and manipulate objects are crucial for many daily activities, such as tying shoelaces or opening jars. Recently, the string-pulling task, which involves cyclically reaching, grasping, and pulling a string, has been used to study coordinated hand movements in rodents and humans. Here, we characterize how adult common marmosets perform the string-pulling task and describe changes in performance across the lifespan. Marmosets ($n = 15$, 7 females) performed a string-pulling task for a food reward using an instrumented apparatus attached to their home-cage. Movement kinematics were acquired using markerless video tracking and we assessed individual hand movements and bimanual coordination using standard metrics. Marmosets oriented their gaze toward the string above their hands and readily performed the task regardless of sex or age. The task required little training and animals routinely engaged in multiple pulling trials per session, despite not being under water or food control. All marmosets showed consistent pulling speed and similar hand movements regardless of age. Adult marmosets exhibited a clear hand effect, performing straighter and faster movements with their right hand despite showing idiosyncratic hand preference according to a traditional food retrieval assay. Hand effects were also evident for younger animals but seemed attenuated in the older animals. In terms of bimanual coordination, all adult marmosets demonstrated alternating movement pattern for vertical hand positions. Two younger and two older marmosets exhibited idiosyncratic coordination patterns even after substantial experience. In general, younger and older animals exhibited higher variability in bimanual coordination than adults.

NEW & NOTEWORTHY Bimanual coordination is crucial for daily activities. In this study, we characterized how common marmosets performed the string-pulling task without extensive training, regardless of sex or age, and naturally exhibited a cyclical alternating pattern of hand movements. Although the overall behavior was similar across ages, younger and older marmosets demonstrated higher variability in bimanual coordination. These results establish the string-pulling task as a reliable tool for studying bimanual coordination and its underlying neural substrates.

bimanual coordination; kinematics; motor control; reach and grasp; string-pulling

INTRODUCTION

Many real-world skills—tying a shoelace, buttoning a shirt, opening a jar—require performing skilled movements with each hand and coordinating the hands toward a common goal (1). Understanding the neural basis of skilled hand movements (2–4) and their bimanual coordination (5) is of central interest in biological motor control, with the bulk of the animal work on this topic focused on dexterous

nonhuman primates, especially the macaque monkey. Despite being less dexterous, recent work in the marmoset monkey demonstrates that they produce sophisticated reaching actions during prey capture in the wild (6). When capturing moving crickets in a naturalistic laboratory setting, marmosets use a power grasp as opposed to a key or precision grip, but their grasp aperture scales with reach velocity and their movements appear to reflect predictive control strategies that compensate for sensorimotor delays (7). These



*M. Bertrand and M. Karkuszewski contributed equally to this work.

Correspondence: J. A. Pruszynski (andrew.pruszynski@uwo.ca).

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results, along with the many behavioral and anatomical similarities between marmosets and more dexterous primates (8–10), suggest that the marmoset may serve as a suitable animal model for studying some aspects of reaching and grasping, which would be attractive given the many practical and technical advantages also afforded by the marmoset model (11–13).

Here, we further this effort by documenting marmoset behavior during unrestrained string-pulling, an ecologically valid behavior that includes both hand movements and bimanual coordination. String-pulling involves making hand-over-hand movements to reel in the string or to acquire a reward attached to the string. It is an established paradigm in comparative psychology, with variations of the task being applied to over 100 species mostly to assess cognitive functions such as means-ends understanding (14). Recently, string-pulling has been used to examine and compare motor control in rodents and humans (15–18). Rodents and humans share many kinematic features when string-pulling, the most striking difference being that rodents rely on tactile cues from the vibrissa to guide their hands to the string, whereas humans use vision to do so. String-pulling may also serve as a clinical biomarker as kinematic metrics appear sensitive and reliable enough to detect movement changes following neurological damage and muscle injury both in humans and animal models (19–23).

We show that marmosets perform the string-pulling task in their group housed home-cage environment without extensive learning, naturally exhibiting cyclical alternating hand movements consistent with previous rodent and human studies (15, 16, 18). Like humans and unlike rodents, marmosets look up at the string above their hands and do not touch it with their face. Notably, our data indicate that, despite showing idiosyncratic hand preferences when retrieving food as has been previously reported (24, 25), adult marmosets produce straighter and faster reaches with their right hand when string-pulling, indicating some degree of motor lateralization. Lastly, we report that individual hand movements are relatively similar between adult, younger, and older marmosets, but that older animals may show weaker lateralization and that both younger and older animals seem to exhibit higher variability in bimanual coordination.

MATERIALS AND METHODS

Subjects

This study was conducted with 15 common marmosets (*Callithrix jacchus*), eight males and seven females, from 6 to 168 mo old (Table 1). Eight adults (4 males, 4 females; 25–60 mo) were used for detailed characterization of string-pulling behavior. To qualitatively investigate age-related changes, animals were divided into three age groups: younger (<24 mo, $n = 4$), adult (as described above), and older (>90 mo, $n = 3$) (26). All marmosets were housed in pairs or groups in a temperature- ($25 \pm 1^\circ\text{C}$) and humidity- ($55 \pm 15\%$) controlled facility with a 12-h light-dark cycle. Marmosets had unrestricted access to food and water. All procedures were approved by the Animal Care Committee of the University of Western Ontario.

Table 1. Marmoset characteristics and hand preferences ($n = 15$ marmosets)

Subject	Sex	Age, mo	Hand Preference	Handedness Index	Proportion Right Hand
Y1	F	6	R	0.62	0.81
Y2	M	12	N/A	N/A	N/A
Y3	M	15	R	0.66	0.83
Y4	F	20	L	−0.97	0.02
F1	F	28	R	0.23	0.62
M1	M	35	Ambi	0.00	0.50
M2	M	38	L	−1.00	0.00
F2	F	49	L	−0.83	0.08
F3	F	53	R	0.27	0.63
M3	M	56	R	0.93	0.97
M4	M	59	R	0.97	0.98
F4	F	59	L	−0.73	0.13
O1	M	110	L	−0.53	0.23
O2	F	114	L	−0.90	0.05
O3	M	168	Ambi	0.10	0.55

Handedness Index

Hand preference was assessed using a simple task where marmosets retrieved a reward (a piece of marshmallow) by reaching through a hole into a box attached to their home-cage. Each trial was scored as left or right based on the hand used. Trials in which both hands were used were excluded. Each marmoset completed 20 trials per session across three sessions, resulting in a total of 60 trials, except for one younger male marmoset (Y2), for whom handedness was not assessed. A handedness index was calculated by subtracting the number of left-handed responses from the number of right-handed responses, and dividing by the total number of responses (27) (Table 1). As such, the handedness index ranged from −1.0 (left-hand bias) to 1.0 (right-hand bias). Marmosets were classified as left-, ambidextrous, or right-handed based on binomial z-scores, calculated from the frequency of left- and right-hand responses. A z-score of −1.64 or lower indicated left-handed marmosets, while a z-scores of 1.64 or higher indicated right-handed marmosets. Intermediate scores were classified as ambidextrous.

String-Pulling Apparatus

Our string-pulling apparatus was based on a previous rodent study (17), using a transparent rectangular box (28 cm × 28 cm × 20 cm) connected to the home-cage. A loop of nylon string (4 mm in diameter) was attached to a continuous four-pulley system, one of which was connected to a rotary encoder to measure string speed. The pulley system was suspended by an aluminum frame constructed from 30 × 30 mm aluminum extrusions (Zyltech). A high-speed camera (240 FPS, GoPro/HERO 8) was facing the animal and collected data for offline analysis. The location of the camera relative to the transparent box was fixed across sessions (Fig. 1A).

The string-pulling task, in which animals had to pull a string to obtain a reward (a piece of marshmallow), was adapted from previous rodent and human studies (15, 16, 18, 28). During 1-wk of habituation, the task was presented once a day for ~20 min and all marmosets spontaneously pulled on the string, then data were collected during 20 min over 5 days. Only trials where the animal was facing the camera

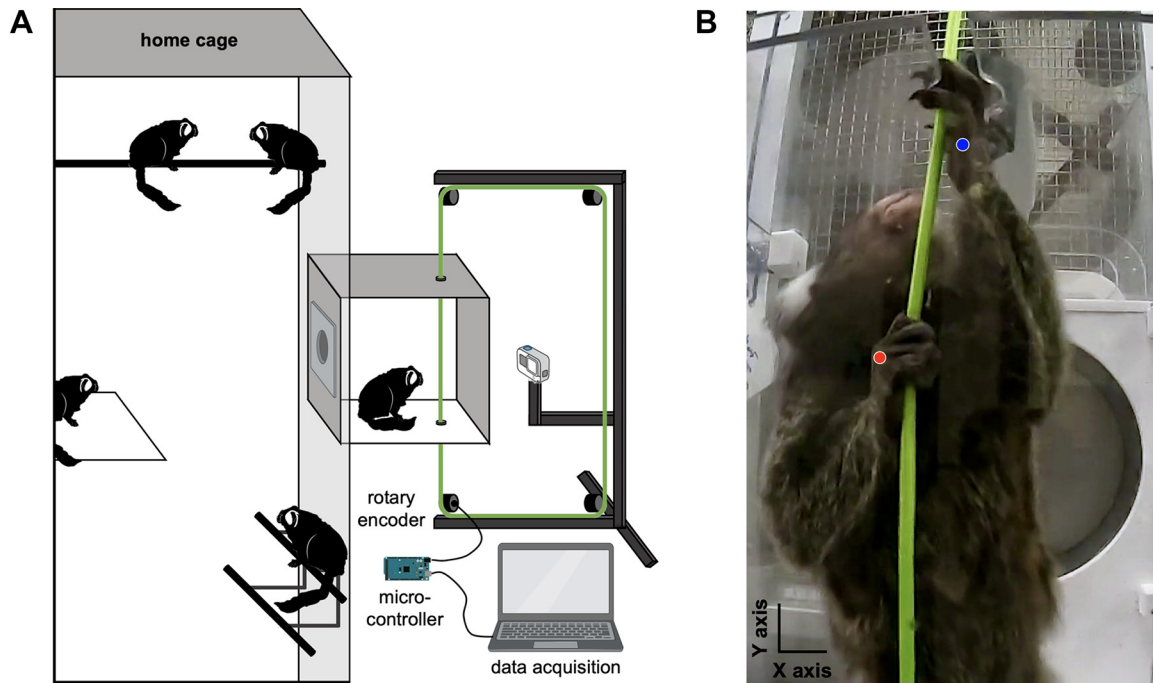


Figure 1. String-pulling apparatus. *A*: schematic of the string-pulling apparatus connected to the home cage. *B*: frame from the string-task. Note the upward gaze toward the reward. Red and blue dots represent the right- and left-hand positions according to the motion-tracking algorithm.

were included, as on other trials, partial occlusions of one hand occurred and could not be used for analysis (average median of excluded trials across all animals: 50%, from 25% to 57%, Supplemental Table S1). Sessions with less than five trials were also excluded. String speed was measured using a two-phase rotary encoder with a resolution of 600 pulses per rotation. Signals from the encoder were processed by a microcontroller (Arduino UNO Rev3, Arduino) to calculate rotation speed, direction (up or down), and length of string pulled. Initial calibration of the number of pulses per millimeter of string pulled was determined by manually pulling the string over a known distance.

Behavioral Analysis

A trial was defined as continuously pulling the string until obtaining an attached reward, ~35 cm directly above the animal such that it could see the reward (Supplemental Video S2). At least 25 trials per animal were included over 5-day sessions. Movement topography and kinematics were averaged across all trials. All postprocessing and filtering were performed using Matlab (R2022b, The MathWorks Inc., Natick, MA) and Python (v. 3.9). Average string speed was extracted from the rotary encoder. Video recordings were trimmed with *ffmpeg* v4.4.2 to contain only the string-pulling behavior. Markerless motion tracking was conducted with DeepLabCut (DLC) (v2.2.0) (29), using a ResNet50 deep convolutional neural network model to extract locations and labels of the nose, string, right hand, and left hand (Fig. 1B). Fifty random video frames from one video per marmoset were extracted (750 total), manually labeled, and used to train the model. After initial training, an extra 150 frames were extracted as outliers (based on the “jump” DLC algorithm, defined as label jumps exceeding 20 pixels in Euclidean distance from one frame to the next) and manually

relabelled. Each iteration of the ResNet50 model was trained for 500,000 iterations and the resultant model was evaluated using the built-in DLC function (average Euclidean error is 5.88 pixels). The known height of the apparatus was used to calculate pixel-to-centimeter conversion. The resulting traces were Butterworth filtered (0.75–9 Hz bandpass).

String-pulling involves a repeated, organized hand-over-hand sequence, consisting of a reaching phase, defined as upward forelimb movement without string contact, and a withdrawing phase, defined as downward movement that includes string contact before releasing the string. In addition, string-pulling cycles were analyzed manually, frame by frame, to identify six segments based on hand shape and location, as described in previous studies in humans and rodents (15–18): lift (raising the hand, partially closed), advance (slight adduction of the hand toward the string, with fingers extended), grasp (flexing the fingers to grasp the string), pull (lowering the string by flexing the lower arm), push (lowering the string by extending the lower arm), and release (extending the fingers to release the string). Like rodent studies, we calculated the correlation between the nose and the string position to see if marmosets used somatosensory inputs from their face to track the string (15, 17).

Following the approach used in a human string-pulling study (18), visual attention, defined as head orientation, and the grasp location were manually assessed frame by frame for all individual reaches of all 15 animals. Two three-point scales were used. For head orientation, scores were assigned as 1 (head is oriented up), 0 (head is straight), and –1 (head is oriented down). For grasp location, scores were assigned as 1 (reaching above the head), 0 (reaching to the level of the face), and –1 (reaching below the level of the face).

Based on previous studies (15–17, 21), and after automatically identified the reach (upward movements) and withdraw (downward movements) phases, we calculated the most commonly used metrics associated with single hand movement during these phases: temporal topography (X and Y coordinates of each hand over time); heading direction [transformation of the origin coordinates (0,0) and the angle of the end coordinates of each hand relative to a polar coordinate system, when 0° is right, 90° is up, 180° is left, and 270° is down]; heading circular variance (measurement of the variability in the heading directions, ranging from 0, where headings are in the same direction, to 1, where headings are uniformly distributed across 360°); Euclidean distance (shortest distance between the start and end of the movement); path circuitry (ratio of the Euclidean distance to actual movement displacement, from 0, most circuitous path, to 1, direct straight line); peak speed (maximum speed in cm/s); average speed (cm/s); and movement scaling [reflecting the isochrony principle where the speed of hand reaching movement increases with more distant targets to keep the reach time approximately constant (30), and is defined as the correlation between peak speeds and Euclidean distances, where a high correlation value close to 1, indicates that peak speed increases with the length of the movement; while a low correlation value close to 0, suggests no scaling between hand speed and movement extent]. Similarly, we calculated commonly used metrics associated with bimanual coordination: hand correlation (horizontal -X and vertical -Y correlation between both hands) and phase shift (temporal displacement of the waveforms of the X and Y hand coordinates).

Statistical Analysis

Statistical analyses were performed using GraphPad Prism 8 (GraphPad Software Inc.). For single-hand metrics in adult animals, three-way ANOVAs were used to analyze the effect of hand, phase, and sex. For bimanual coordination metrics, Wilcoxon signed-rank tests were used to compare each median with zero. Pearson correlations were calculated to investigate the association between age and

string speed. Differences were considered statistically significant if $P < 0.05$.

RESULTS

The string-pulling apparatus was mounted to the home cage of a group-housed set of marmosets (Fig. 1). After a short habituation period, marmosets willingly entered the apparatus. Only one marmoset was allowed to enter the apparatus at a given time. Access to the apparatus was controlled by the experimenter via a sliding door at the entrance. Once inside, the marmoset remained in the apparatus until it showed no further interest in performing the task, at which point the sliding door was opened and it could return to its home cage. String-pulling was always done in full-light conditions and no attempts were made to alter the normal housing setup or the arrangement of the room, which included multiple home cages.

String-Pulling Behavior in Adult Marmosets

All eight adult marmosets spontaneously engaged in the string-pulling task, often from their very first exposure. Adult marmosets seemed to perform the task guided by vision, almost always orienting their heads upward (median for all reaches across adults: 93%, range 89–100%). Like humans (18), marmosets appeared to keep their gaze on the string above the grasp point since, while the head was oriented upward, they mostly grasped either at the level of the face or just below the level of the face (median for all reaches across adults: 70%, range 55–87%) (Supplemental Video S2, and Figs. 1B and 2A). We found no correlation between marmoset nose position and string position in the horizontal direction (median correlation across animals: $r = -0.008$, Wilcoxon signed-rank test against zero: $P = 0.13$). That is, like humans and unlike rodents (15, 16), marmosets did not appear to use somatosensory inputs from their face to guide the string.

In terms of individual hand movements, string-pulling in adult marmosets was qualitatively similar to what has

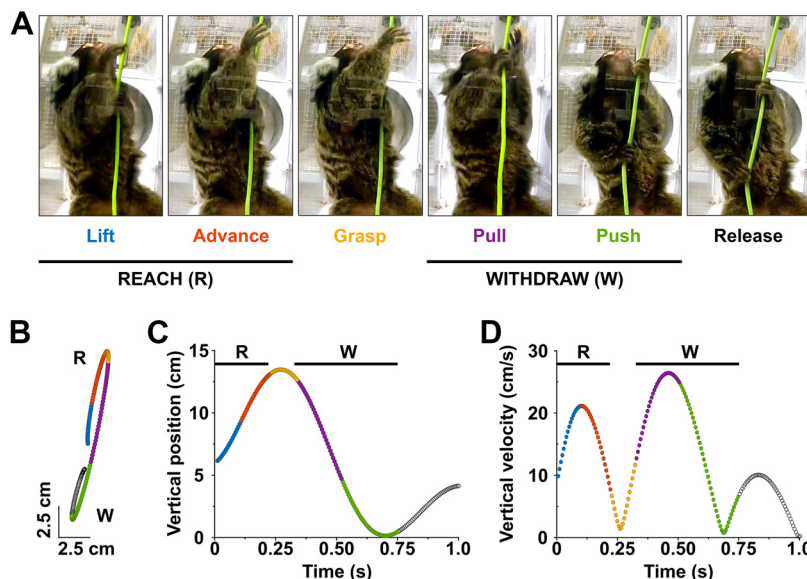


Figure 2. Example of a single string-pulling cycle for the right hand. A: sequence of six movement segments during string pulling: Lift (blue), the hand is raised; advance (orange), hand is extended toward the string; grasp (yellow), fingers are flexed to grasp the string; pull (purple), the string is lowered by flexing the lower arm; push (green), the string is lowered by extending the lower arm; release (black), fingers are opened and extended to release the string. The reach phase (R) is defined as upward movements without string contact (lift and advance), the withdraw phase (W) is defined as downward movements with string contact (pull and push). Note the gaze directed on the string, above the grasp point. B: spatial segmentation of the six segments. Dots are plotted every 6 ms. C: vertical position of the segments over time. Data are aligned on the beginning of lift. D: speed of the segments over time.

previously been described in mice, rats, and humans. Marmosets showed the typical reach-and-withdraw cycle, with a reach phase involving upward movements to grasp the string without string contact and a withdraw phase involving downward movements while grasping the string before releasing it. Marmoset grasp aperture opened during the reaching phase and generally started to close before contact was made with the string (Figs. 1B and 2A).

We divided each reach cycle into six segments based on hand position and orientation: lift (raising the hand, partially closed), advance (slight adduction of the hand toward the string, with fingers extended), grasp (flexing the fingers to grasp the string), pull (lowering the string by flexing the lower arm), push (lowering the string by extending the lower arm), and release (extending the fingers to release the string) (Fig. 2A). Typically, hand speed increased before grasping the string, peak reach speed occurred near the transition between the lift and advance phases, approached zero during the grasp phase, increased again during the push and pull phase of the withdrawal and approached zero during release (Fig. 2, B–D).

We characterized several standard metrics (see MATERIALS AND METHODS) to compare the reach and withdraw phases of the left and right hand across male and female marmosets. First, we calculated the heading direction of the movement trajectories, defined as the end point of the trajectory when the string is grasped during the reach phase and released during the withdraw phase (Fig. 3A). In addition to moving in opposite directions for the reach and withdraw phases (as required by the task), marmosets moved their hands across their body for both phases, as their hands crossed the midline, yielding a reliable difference in heading direction between hands (main effect of hand: $F_{1,12} = 19.63$, $P =$

0.0008), which did not differ between males and females (main effect of sex: $F_{1,12} = 0.064$, $P = 0.80$).

Second, we examined movement consistency by calculating the circular variance of heading trajectory across reaches (Fig. 3B). Marmosets were very consistent, exhibiting a low variance, and even more consistent with the right hand than the left hand (main effect of hand: $F_{1,12} = 21.38$, $P = 0.0006$). This consistency was similar across phases (main effect of phase: $F_{1,12} = 0.35$, $P = 0.57$) and as a function of sex ($F_{1,12} = 0.66$, $P = 0.43$).

Third, we calculated path circuitry, a measure of movement straightness (Fig. 3C). Although adult marmosets showed relatively straight movement trajectories, right-hand trajectories were consistently straighter than left-hand trajectories (main effect of hand: $F_{1,12} = 17.81$, $P = 0.001$). Straightness was not reliably different between reach and withdraw phases (main effect of phase: $F_{1,12} = 1.41$, $P = 0.26$) or between males and females (main effect of sex: $F_{1,12} = 0.56$, $P = 0.47$).

Fourth, we calculated peak and average pulling speed (Fig. 3, D and E). All adult marmosets pulled faster with their right hand (main effect of hand: peak speed: $F_{1,12} = 80.37$, $P < 0.0001$; average speed: $F_{1,12} = 68.14$, $P < 0.001$) and even somewhat faster during the withdraw phase for their right hand (hand-by-phase interaction: peak speed: $F_{1,12} = 4.79$, $P = 0.049$; average speed: $F_{1,12} = 6.22$, $P = 0.03$). Like the other metrics, we observed no reliable difference between males and females (main effect of sex: peak speed: $F_{1,12} = 0.004$, $P = 0.95$; average speed: $F_{1,12} = 0.58$, $P = 0.46$).

Fifth, we calculated movement scaling, the correlation between peak speed and the Euclidean distance of each movement (Fig. 3F). All marmosets demonstrated high value of movement scaling, adapting the velocity to the length of

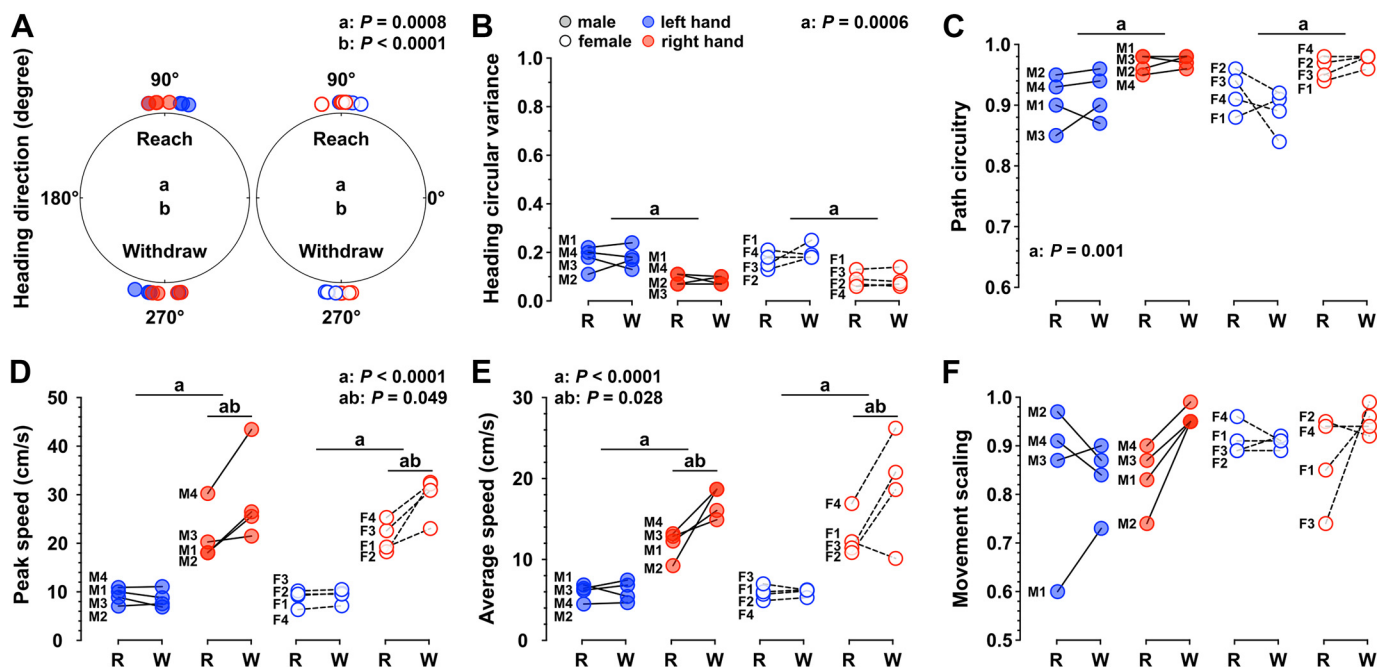


Figure 3. Single-hand metrics. Comparison of metrics for the left (blue) and right (red) hand during the reach (R) and withdraw (W) phases, shown separately for males (M, filled dots with solid lines, $n = 4$) and females (F, dots with dotted lines, $n = 4$). Results of the three-way ANOVA: ^amain effect of hand; ^bmain effect of phase; ^{ab}hand-by-phase interaction. Medians over 5 sessions of A: heading direction, B: heading circular variance, C: path circuitry, D: peak speed, E: average speed, and F: movement scaling are presented for each marmoset.

the movement, and scaled their movements similarly (main effect of sex: $F_{1,12} = 2.26$, $P = 1.16$), with both hands (main effect of hand: $F_{1,12} = 1.42$, $P = 0.26$) and for both phases (main effect of phase: $F_{1,12} = 3.64$, $P = 0.08$).

We characterized bimanual coordination by examining the relationship between horizontal and vertical trajectories across the hands, during the combined reach and withdraw phases. We found in-phase horizontal movements between hands (Fig. 4, A, C, and E), presumably reflecting the general need to move the hands together to account for the shifting horizontal position of string over time. We also found largely antiphase vertical movements (Fig. 4, B, D, and F), representing the alternating movements that define the cyclical string-pulling action.

String-Pulling across the Lifespan

We examined string-pulling behavior in a small number of younger (<24 mo old) and older marmosets (>90 mo old) in our colony. The main goal of examining these groups was to establish whether they could perform the task as motivation

for future developmental and aging studies. Given the small sample size, we did not perform the same statistical analysis as for the adults but presented the results in a similar fashion for qualitative comparison.

Like the adults, both younger and older marmosets spontaneously performed the string-pulling task. Although all animals readily learned the task, it took more training days to obtain five sessions for older marmosets because they were less likely to produce the number of required string-pulling trials early in training. The limiting factor with respect to learning appeared to be motivation rather than movement control. Like adults, younger and older marmosets oriented their heads upward (younger marmosets median across all reaches: 94%, range 94–99%; older marmosets median across all reaches: 98%, range 95–98%); and reach mostly at the level of the face or just below the face (younger marmosets median across all reaches: 70%, range 62–94%; older marmosets median across all reaches: 66%, range 38–81%). After habituation, we found no reliable correlation between age and average string speed (Pearson $r = 0.35$, $P = 0.20$;

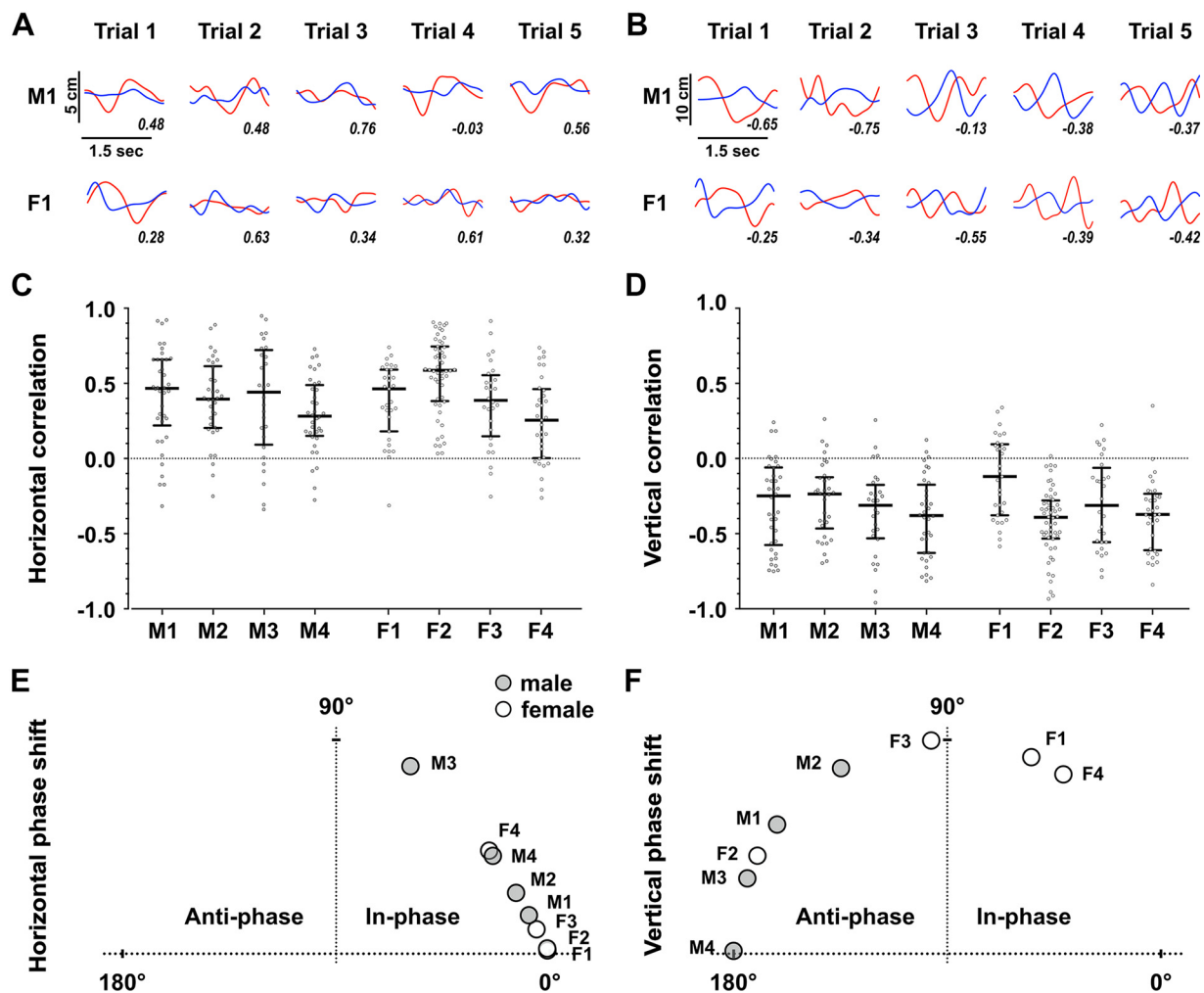


Figure 4. Bimanual coordination. Example of five matching trials showing the horizontal x-axis (A) vertical y-axis (B) positions of the left (blue) and right (red) hand for a male (M1) and a female (F2) marmoset, with corresponding correlation values. Medians over 5 sessions of horizontal (C) and vertical (D) correlations between left and right hands, with data points for each trial for each male (M, $n = 4$) and each female (F, $n = 4$) marmosets. Median of horizontal (E) and vertical (F) circular phase shift representing the in-phase and anti-phase movements between left and right hands for each marmoset.

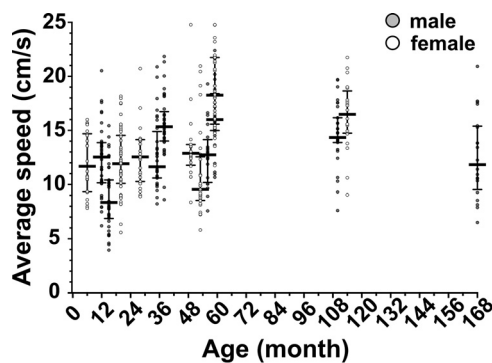


Figure 5. String pulling speed across the lifespan. String speed as extracted from a rotary encoder for each marmoset. The individual dots represent single trials over 5 sessions. The horizontal line represents the median for each animal ($n = 15$ marmosets).

(Fig. 5). Even our oldest animal pulled faster than some adult animals.

Using the same single-hand metrics as for the adult marmosets above, we quantified the reach and withdrawal phases of each hand for younger and older marmosets, which generally showed the same trends as the adult animals (Fig. 6). Younger and older animals appeared to make hand movements across their body for both reach and withdrawal phases (Fig. 6A). Both groups appeared to exhibit greater movement consistency for the right hand than the left hand, though this lateralization might have been reduced in the older animals (Fig. 6B). Reduced lateralization was also apparent in movement straightness (Fig. 6C). On the other hand, similar to the adults, younger and older animals increased movement speed with the right hand in general (Fig. 6, D and E), and scaled their hand peak speed with the movement extent (Fig. 6F).

With respect to bimanual coordination, both younger and older marmosets displayed the typical cyclical string-pulling behavior, generally showing in-phase horizontal movements

(Fig. 7, A and C) and antiphase vertical movements between hands (Fig. 7, B and D). However, some of these animals also exhibited more variable and idiosyncratic coordination patterns, with no significant positive correlations in horizontal movements (Y2: $P = 0.27$) (Fig. 7C), and/or no significant negative correlations in vertical movements (Y1: $P = 0.26$; O1: $P = 0.37$; O3: $P = 0.09$) (Fig. 7D).

DISCUSSION

Our study provides the first characterization of string-pulling in the common marmoset. We show that marmosets, like rodents and humans, perform the string-pulling task with minimal training and naturally exhibit a cyclical alternating pattern of hand movements (15–18). Like humans, but unlike rodents, marmoset string-pulling appears to be driven by vision (15, 16, 18), keeping their head oriented upward while grasping either at the level of the face or below it. Interestingly, despite showing idiosyncratic hand preferences when reaching for food, adult marmosets show lateralization in their individual hand metrics during string-pulling, producing straighter, faster, and less variable kinematics with their right hand. The extent to which this lateralization arises because of the current unconstrained setup and the use of a single front-facing camera setup requires further investigation to draw definitive conclusions. Our findings suggest some age-related changes during string-pulling. Although the overall behavior is quite similar between adult, younger, and older marmosets, both younger and older animals demonstrate higher variability with respect to bimanual coordination. Older marmosets may have reduced lateralization in individual hand metrics.

The String-Pulling Task for Marmoset Motor Neuroscience

Studies on bimanual coordination in primates usually focus on hand preference using tasks such as the tube task,

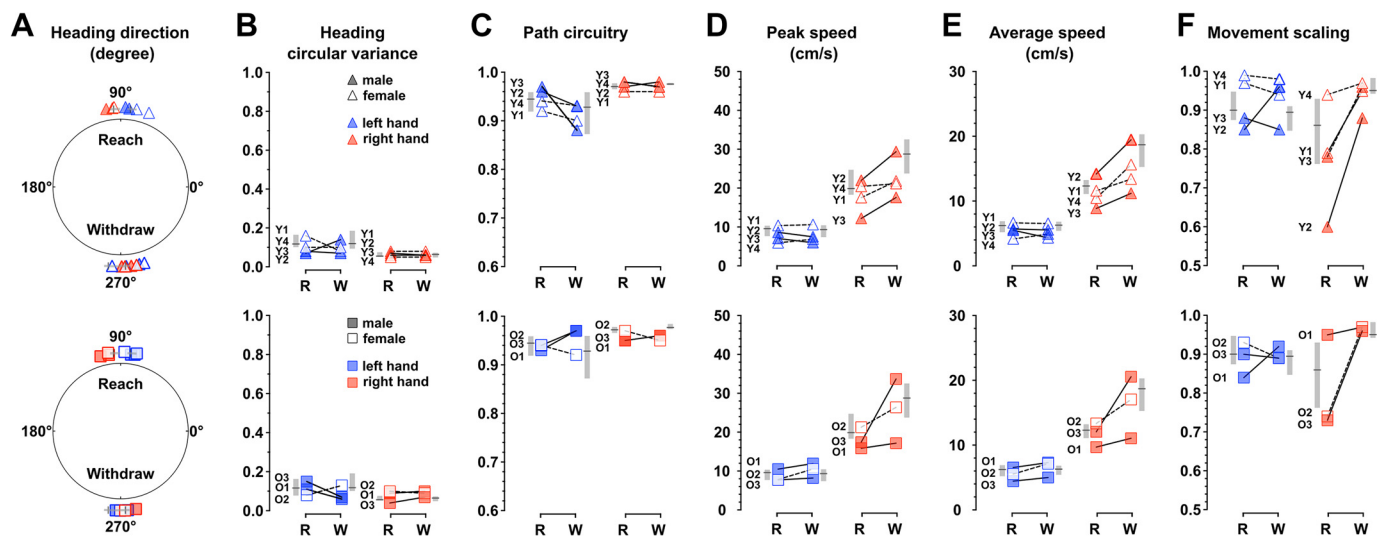


Figure 6. Single-hand metrics across the lifespan. Left (red) and right (blue) hand metrics for younger (Y, <24 mo, $n = 4$) and older (O, >90 mo, square, $n = 3$) marmosets during the reach (R) and withdraw (W) phases. Medians over 5 sessions of heading direction (A), heading circular variance (B), path circuitry (C), peak speed (D), average speed (E), and movement scaling (F) are shown for younger (triangle, top) and older (square, bottom) marmosets. Gray lines and bars on the side of each metric represent median values and interquartile range for adult marmosets ($n = 8$).

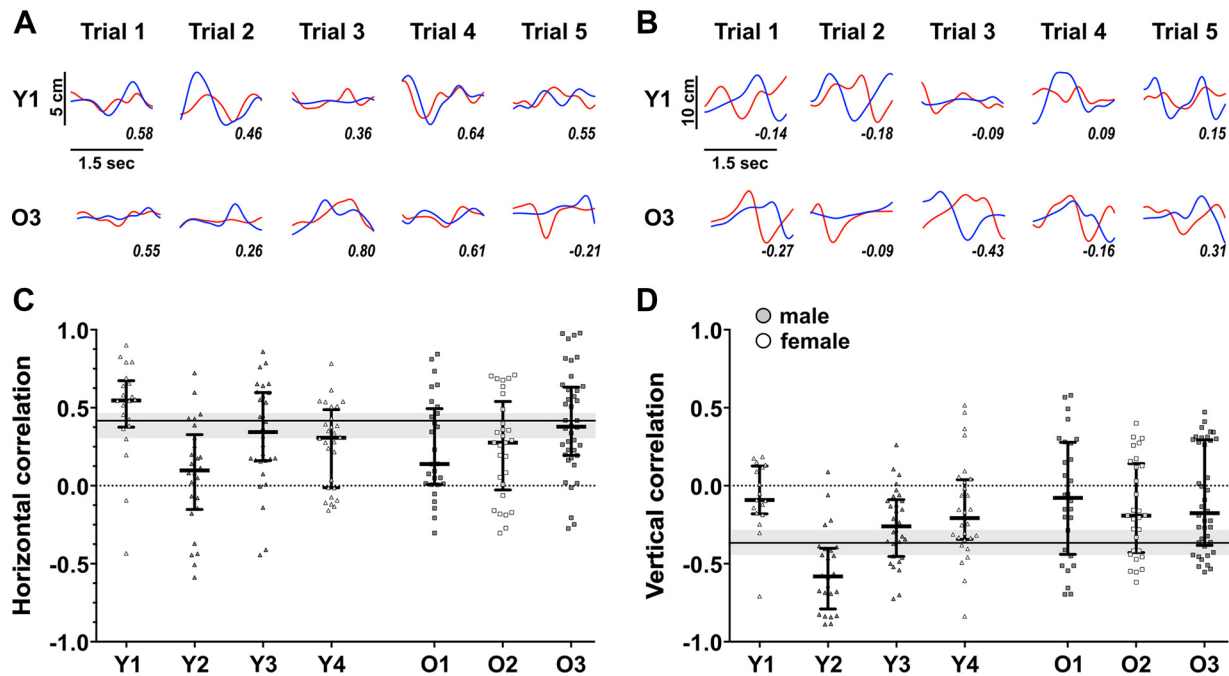


Figure 7. Bimanual coordination across the lifespan. Example of five matching trials showing the horizontal x-axis (A) and vertical y-axis (B) positions of the left (blue) and right (red) hand for one younger (Y1) and one older (O3) marmoset, with corresponding correlation values. Medians over 5 sessions with interquartile range of horizontal (C) and vertical (D) correlations between both hands, with data points for each trial for each younger (Y, <24 mo, triangle, $n = 4$) and older (O, >90 mo, square, $n = 3$) marmoset. Black line and gray bar represent median and interquartile range from adult marmosets ($n = 8$).

Brinkman board tasks, or box task, where one hand stabilizes while the other retrieves a reward (31–34). More recently, the cycling task (35), which requires a monkey to hold one or two manipulanda and to cycle them, has been introduced to study bimanual coordination. However, these tasks do not fully reflect the natural behavioral repertoire of primates. Naturalistic bimanual behaviors, such as feeding (36), tool use in the wild (37), and gesturing (38), have also been studied. Although they provide valuable insights into how primates use their hands in their natural environment, they often lack the experimental control required for detailed analysis of coordination patterns.

The string-pulling task has several key features, over and above the fact that it includes both hand movements and bimanual coordination, which make it an attractive task for studying the neural control of movement in the marmoset monkey. String-pulling, like cricket catching (7), is a well-controlled task that requires little to no training, presumably because it mimics ecologically conserved behaviors like climbing or foraging (14, 39). Indeed, male and female marmosets of all ages spontaneously engaged in the task within a week of first exposure even though they were under no water or food restriction. The ecological validity of the task may explain the relative similarity of the behavior across the lifespan compared with previous reports using tasks with higher cognitive and motor demands (40–43). Although the basic string-pulling task may be an advantage when investigating some motor changes with aging, revealing the full spectrum of age-related decline likely requires more complex or difficult variants, such as changing the string texture, tension, or thickness.

Indeed, string-pulling affords many manipulations that are of direct relevance to sensorimotor neuroscience. For example, manipulating string thickness provides a way of studying the control of grasp aperture (44, 45) and online planning (46–48). Changing the tension on the string or the texture of the string provides a way of studying the coordination of grip and load forces (49, 50), inducing motor learning (51), and/or probing fast feedback responses to visual or mechanical perturbations (52–54). Such manipulations are powerful because they require different control strategies, and as they do not change the natural string-pulling behavior, they can likely be enacted quickly if not in real-time, which is not generally the case in more abstract experimental settings.

As demonstrated here, string-pulling is readily amenable for in-cage studies, which makes it possible to not only study unconstrained behavior but also assess relatively large cohorts of marmosets, as is often needed for studying disease models and testing clinical interventions. However, this minimally controlled environment, with unconstrained animals and high movement freedom, limited the number of trials we could include. More trials will be essential for conducting more complex neurophysiological studies. Our ongoing work indicates that chair-restrained and head-fixed marmosets can still perform the string-pulling task and produce more trials in this context. Future studies in this more controlled setting and with a multicamera tracking setup will open up more precise experiments, and a host of more sophisticated methods including large-scale electrophysiology via acutely inserted Neuropixel electrodes (55, 56) or Myomatrix arrays (57), as well as calcium imaging (58) and optogenetic stimulation (59).

String-Pulling Movements

All marmosets appeared to use vision to track the string, but they directed their gaze above their hands and generally did not look at the grasp point. This behavior is similar to human string-pulling, where participants focus their gaze at the grasp point only when they are asked to reach for a specific cue and otherwise look up at the string above their hands (18). The observation that marmosets, like humans, do not fixate on the grasp point, indicates that they rely on somatosensory inputs—both the tactile events that occur when string contact is made and proprioceptive signals about joint configuration—to guide their hands to the string. Mice and rats must also use somatosensory inputs to guide their hands as they grasp the string in an unseen location below their snout (15, 16). Interestingly, unlike marmosets and humans, rodents keep their snout and vibrissae in constant contact with the string. These vibrissae inputs in rodents, like visual inputs in primates, may provide online tracking of string position.

Marmoset string-pulling behavior involved hand-over-hand cycling movements with distinct reach and withdraw phases. Related studies in rodents and humans have identified a similar six-segment sequence within the reach and withdraw phases (lift, advance, grasp, pull, push, release) characterized by specific trajectories, arm movements, and hand shapes (15–18). However, unlike one recent rat study (17) where segment identification was automated, the different segments were identified manually, similar to the other string-pulling studies (15, 16, 18), which limits scalability and needs to fully take advantage of the in-cage approach. Nonetheless, our results suggest that grasping strategies differ across species. Rodents use an arpeggio grip, first contacting the string with extended fingers, then closing all fingers at once based on somatosensory feedback (15, 16, 60). Humans, by contrast, use a whole hand grip, fully opening all fingers before the grasp, contacting the string with fingers 5 (pinky) and 4 to guide it toward the palm while sequentially closing the digits from fingers 5 to 1 (thumb) to hold the string (18).

Previous studies have shown that marmosets typically use a power grasp (16, 61, 62), preshaping the hand by moving all fingers simultaneously before object contact and closing them around the object and pressing it against their palm. However, whether they scale their grip according to the size of the target remains debated (7, 62, 63). We observed a similar power grasp pattern, but our results cannot address the issue of scaling directly as we did not manipulate string thickness, and our use of a single frontal camera limited our analysis to relatively gross whole arm effects.

Adult marmosets exhibited direct, scaled, and consistent movements, with faster movements during the withdraw phase than the reach phase. This may result from a different utilization of gravitational force during reach (against gravity) and withdraw (with gravity) movements (64–66). Studies have shown longer acceleration during downward movements compared with upward movement of equivalent duration and amplitude (67, 68). Although our present setup did not allow for it, it would be relatively straightforward to test this idea by having marmosets perform the string-pulling behavior in a horizontal apparatus, where the effects of gravitational force are limited. Lastly, marmosets stabilize their posture by pulling the string during the withdraw

phase, which likely contributes to faster movements compared with the reach phase, where their hands move freely.

Marmoset Handedness

Although we did not observe a systematic bias in animal posture, some caution should be taken when interpreting kinematic differences between hands as our setup is relatively unconstrained, allowing marmosets to pull from varying orientations, and our analysis is based on video from a single front-facing camera that cannot resolve out of plane movements, introducing potential biases in the measurements. That said, we found that adult marmosets showed straighter, faster, and less variable movements with their right hand. This systematic right-hand “advantage” in terms of movement characteristics did not correlate with a standard hand preference assay (27) which, consistent with most previous work (24, 69–71), showed that about half of the marmosets in our sample had a right-hand preference. The disconnect between movement features and hand preference may partly reflect known postural effects on hand preference. Right-hand use in some primates is increased for bipedal reaching compared with quadrupedal reaching (72) and our string-pulling task was performed in bipedal posture, whereas the food preference assay was generally performed from a quadrupedal posture (73). Interestingly, no equivalent hand-specific effects were reported in rodent string-pulling studies (15–17), despite evidence of hand preferences and brain asymmetry (74–76). In human string-pulling, not all parameters reported here were examined but asymmetrical hand movements were only observed when the task was performed from memory and these were not hand specific (18).

The relationship between brain lateralization, where each hemisphere exerts preferential control over certain behavioral functions (77–79), and handedness, which refers to the preferred hand for doing manual tasks (80, 81), has been largely studied in humans (82–85). One prominent idea is that sensorimotor lateralization is related to the functional specialization of each arm for different functions (86–91). For example, right-handed patients with left hemisphere damage after a stroke show deficits in arm trajectory control and joint coordination, whereas right-handed patients with right hemisphere damage show deficits in movement accuracy (92). Such hemispheric specialization in different hand metrics may be linked to the hand effect we report. However, our findings indicate that the specialization underlying hand preference can be decoupled from the specialization responsible for hand-specific movement characteristics. How this relates to humans is hard to say given the very strong population bias toward right-hand preference compared with other animals and the relative paucity of studies on human left-handers. That said, the studies that exist in this context suggest that lateralization with respect to hand preference and hand movement characteristics are related in that left-handers show an inverted pattern of movement characteristics, though this inversion is not as strong and not completely symmetrical (93, 94). Lastly, our data suggest that the hand effect on movement characteristics is somewhat weaker for the older marmosets. Such a result, if born out with a properly powered sample, would be consistent with previous human studies showing a decrease in hemispheric

asymmetry in older adults (95–98) and thus provide an experimental window into its underlying neural mechanisms.

Conclusion

In the present study, we characterized how common marmosets performed the string-pulling task. Marmosets completed the task regardless of sex or age, without extensive learning, and naturally exhibited a cyclical alternating pattern of hand movements. This study paves the way for using string pulling as a useful paradigm for studying the neural control of reaching and grasping, as well as bimanual coordination.

DATA AVAILABILITY

Data will be made available upon reasonable request.

SUPPLEMENTAL MATERIAL

Supplemental Table S1: <https://doi.org/10.6084/m9.figshare.28661423.v1>.

Supplemental Video S2: <https://doi.org/10.6084/m9.figshare.28661468.v1>.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

M.B., M.K., R.K., J.-J.O.d.X., and J.A.P. conceived and designed research; M.B. and M.K. performed experiments; M.B. and M.K. analyzed data; M.B., M.K., R.K., J.-J.O.d.X., and J.A.P. interpreted results of experiments; M.B. and J.A.P. prepared figures; M.B. drafted manuscript; M.B., M.K., R.K., J.-J.O.d.X., and J.A.P. edited and revised manuscript; M.B., M.K., R.K., J.-J.O.d.X., and J.A.P. approved final version of manuscript.

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