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String-pulling for food by the rat: Assessment of movement, topography and kinematics of a bilaterally skilled forelimb act

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ABSTRACT

A variety of behavioral tests have been developed to assess skilled forelimb function in the rat, including tests that assess use of a single limb in reaching for food and placing it in the mouth for eating. The present study describes bilateral hand use in string-pulling to obtain a food reward. The movement consists of alternating forelimb movements in which a limb is advanced to grasp a string and withdraw it toward the body in order to retrieve a food reward. The movements of aim, advance, grasp, pull and push are associated with hand shape changes including collect, overgrasp, grasp and release. The topography and kinematics of limb and hand movement are assessed by digitizing methods that derive trajectory, distance, and velocity measures. The task is acquired by a rat within a few days of training, features few missed grasps, shows improvements with practice, and yields dozens of independent reaches by each hand in a single test session. The present analysis provides simple methods for describing each independent forelimb and hand movement and its topographic and kinematic properties. The similarities between string-pulling and other rat forelimb movements are discussed in relation to the idea that rat forelimb movements are conserved in tasks such as string-pulling, walking, reaching for food and grid walking. The task is also discussed with respect to its potential to investigate neural and cognitive bases of fine motor control.

1. Introduction

Beginning with Köhler's (1927) demonstration that apes display insight learning in adapting objects to serve as tools for retrieving a food reward, there have been many demonstrations of tool or prototool use in animals. One example of prototool use is string-pulling, in which an animal pulls on a string to gain a food reward attached to its end. String-pulling has been taught to or spontaneously displayed by a wide range of animal species (Kolb, Cioe, & Comeau, 2008; Osthaus, Lea, & Slater, 2005; Wishaw, Tomie, & Kolb, 1992; Whitt, Douglas, Osthaus, & Hocking, 2009). It is very likely that string-pulling falls within the natural repertoire of many animals because it is akin to pulling on nesting material, pulling on a food object that an animal wants to retrieve, pulling on a branch that might contain a food item, or pulling on a tall blade of grass that contains seeds on its end. In a typical string-pulling act, an animal pulls on a long piece of string in order to reel in a food reward tied at the end. String-pulling behavior has been used to investigate a range of cognitive processes (for review see Jacobs & Osvath, 2015). For example, combining string-pulling with visual discrimination learning has provided insight to the variability in means-end learning observed among different species of parrots (Krashennikova, Bräger, & Wanker, 2013). Rats have been trained to use olfactory and tactile cues during string-pulling behavior to

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investigate the neurobiology of mnemonic function (Köppen et al., 2016; Whishaw & Tomie, 1991). String-pulling behavior has also been adapted for bumblebees to investigate social learning (Alem et al., 2016).

The adaptability of string-pulling behavior has provided a robust tool for comparative cognition; however, research has yet to characterize the organization of the fine motor movements used by the rat for string-pulling behavior. In the present study a combination of measurement approaches are used to investigate rat string-pulling. It has been argued that human and non-human primate manipulatory scale voluntary movements depend on a hand-centered representational system (Gordon, Ghilardi, & Ghez, 1992). Electrophysiological (Brown & Testkey, 2014; Graziano, 2008; Kaas, Gharbawie, & Stepniewska, 2013) and behavioral (Gordon, Ghilardi, & Ghez, 1994, Gordon, Ghilardi, Cooper, & Ghez, 1994) approaches have provided evidence that this representational system separately encodes the type of movement as well as the movement's direction and distance. Provided that a similar representational system is conserved in rats, then components of string-pulling behavior should exhibit organizational characteristics consistent with direction and distance estimation. For example, human participants modify their manipulatory scale movement kinematics (peak speed) to the extent of the movement (Gordon, Ghilardi, Cooper et al., 1994). A similar relationship has been observed in rat ambulatory scale exploratory behavior (Wallace, Hamilton, & Whishaw, 2006). It remains to be determined if this relationship is observed in movements at the rat manipulatory scale.

The current study uses qualitative and quantitative analysis techniques to investigate the movement organization associated with string-pulling behavior in rats. Qualitative analysis involves characterizing forelimb and hand movements engaged during string-pulling. Quantitative analysis uses motion capture software to investigate the topographic and kinematic characteristics of the functional units that emerged from the qualitative analysis. The results of this work establish a foundation for future research to investigate manipulatory scale movement organization observed across a variety of animal species.

2. Materials and methods

2.1. Subjects

Male Long Evans rats ($n = 5$) were obtained from the Northern Illinois University vivarium at 90 days of age and group housed in opaque plastic cages with wire mesh tops. Throughout testing rats were maintained at 85% of their ad lib weight, and the colony room was maintained at 20–21° with 12-h light/dark cycle. All experimental protocols were approved by the NIU Institutional Animal Care and Use Committee. These naïve rats were a subset of the animals in a larger project investigating the effects of cortical devascularization on fine motor control.

2.2. Apparatus

A rectangular transparent cage (46 cm × 26 cm × 26 cm) with a wire mesh top and an opaque barrier restricting access to half the cage served as the string-pulling apparatus (see Fig. 1). The apparatus was placed on table in a small room with many visual cues. The string (0.2 cm in diameter) was 100% cotton that varied length from training (100 cm) to testing (150 cm) with a weight attached to the end of the string in the cage, preventing the string from falling out of the apparatus. A JVC HD video camera (Model #: GY-HM100U) was positioned perpendicular to the wall of the apparatus with the string. The resulting videos were stored on DVDs for subsequent offline analysis.



Fig. 1. Photo of the apparatus with a subset of the strings used during training (left panel) and testing (right panel).

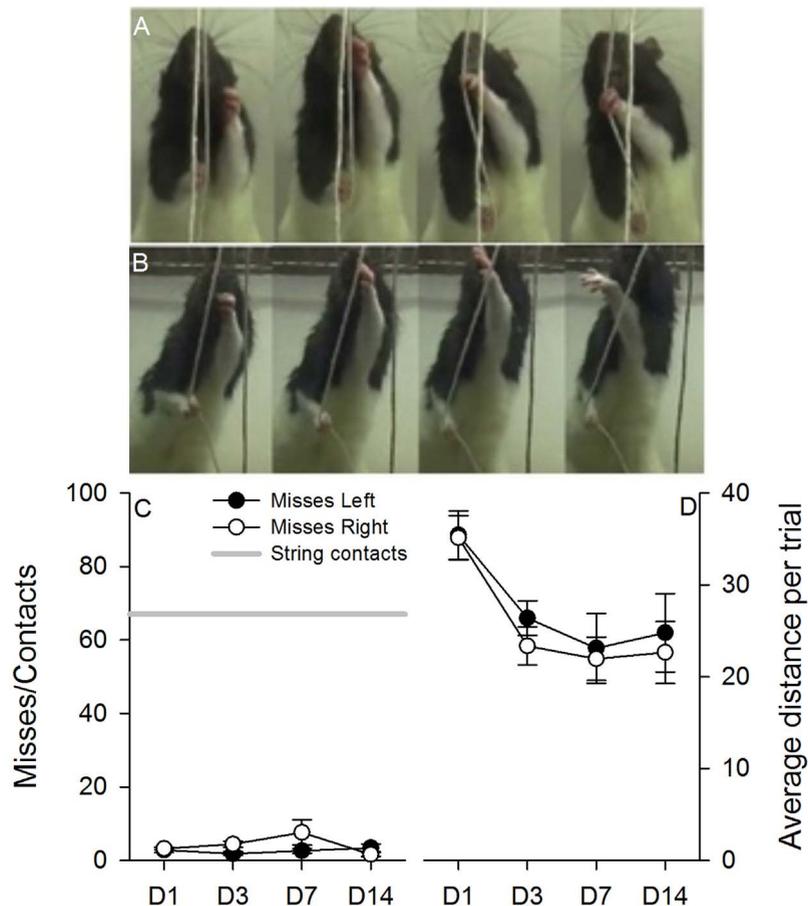


Fig. 2. Sequences of video frames illustrate a correct contact with the string (panel A) and a missed (panel B) contact with the string. The estimated number of string contacts (grey line) and average number of missed string contacts for all trials within a day is plotted for right (white circles) and left (filled circles) limbs across testing days (see panel C). Average distance each forelimb traveled per trial is plotted for both limbs across testing days (see panel D).

2.3. Procedures

String-pulling behavior was shaped over several days. On the first day of training, rats were individually placed in the string-pulling apparatus without the barrier. Twenty strings of varying length (30 cm–100 cm) were hung into the apparatus and half were baited with a small piece of cashew. Rats were left in the apparatus until all the strings were pulled in or an hour had elapsed. If a rat failed to pull all the strings within an hour, an additional 20 strings (10 baited) were hung over the edge of their home cage overnight. The next day, rats were given eight trials to pull a 100 cm string to retrieve a piece of cashew. Rats continued daily training with the 100 cm string until successfully retrieving the cashew on all eight trials. After reaching criteria, the string length was extended to 150 cm for all eight trials. Testing began the first day after the cashews were successfully retrieved on all trials with the 150 cm string. Each testing session involved eight trials with the 150 cm string baited with a cashew. String-pulling testing occurred the first, third, seventh, and fourteenth days after the last day of training. After a rat completed a training or testing session the apparatus was wiped down with ammonia based cleaner and dried prior to running the next rat. Strings were replaced daily.

2.4. Behavioral analysis

String-pulling is an organized sequence of forelimb movements. Each forelimb makes repeated contacts with the string during a trial (see panel A of Fig. 2). On an occasion the forelimb will miss contacting with the string (see panel B of Fig. 2). Each missed contact with the string observed for all of the trials within a day were recorded and served as an assessment of the accuracy of movements. The efficiency in reaching the cashew was quantified as the distance a forelimb traveled on a single trial. Peak Performance (Vicon, Denver, CO, USA) motion capture software was used for frame-by-frame (30 Hz) analysis of string-pulling behavior. Samples of string-pulling behavior were obtained from trials two, five, and eight from each testing day. The position of the forelimb during string-pulling behavior was digitized by selecting the pixel that corresponded to the center of the right and left hand for each frame of video. The resulting set of x- and y-coordinates were used to calculate the distance each forelimb traveled during the three sample trials per day.

Frame-by-frame analysis revealed that string-pulling behavior can be segmented based on function/topographic components of movement. Each limb cycled through reach and withdraw phases of movement. The reach phase was defined as upward forelimb movement without string contact. In contrast, the withdraw phase was defined as downward movement that included string contact. These topographic characteristics were used to segment each set of forelimb x- and y-coordinates into reaches and withdraws.

Several measures were developed to investigate the topographic organization of reach and withdraw phases. First, each phase represents a path through manipulatory space and these paths may vary in circuitry. Path circuitry of a component was calculated by dividing the Euclidean distance (shortest distance between the start and end of the path) by the total distance. As the values of this ratio range from 0.0 (circuitous) to 1.0 (non-circuitous). Next, the movements for each reach and withdraw phase is oriented in a specific direction. The heading direction of movement was calculated by transforming the start and end coordinates of the path such that the start of the path is the origin (0,0) and the angle of the end coordinate is calculated relative to a polar coordinate system (0°: right; 90°: up; 180°: left; 270°: down). The parameter of concentration is a circular statistic (Batschelet, 1981) that can quantify the within day variability in headings for a set of reaching or grasping phases. Values of the parameter of concentration range from 0.0 (headings are uniformly distributed across 360°) to 1.0 (headings are in the identical direction). Finally, the average direction of movement was calculated for each set of reach and withdraw phases across days.

Kinematic characteristics of reach and withdraw phases were also investigated using several measures. First, the peak moment-to-moment speed was recorded and averaged for reach and withdraw phases across days. Next, the Euclidean distance was recorded and averaged for reach and withdraw phases across days. Finally, previous research has demonstrated that humans (Gordon, Ghilardi, Cooper et al., 1994) adjust their manipulatory scale peak speeds to the extent of movement. This movement scaling was quantified as the correlation between the set of peak speeds and Euclidean distances obtained from each reach and withdraw phase across days.

Within Subjects ANOVA was used to investigate changes in performance across forelimb (right vs. left), testing days (d1, d3, d7, d14), and phases (reach vs. withdraw) of string-pulling behavior. Linear trend analyses were used to evaluate systematic changes in performance across days.

3. Results

3.1. Reach accuracy

Rats readily engaged in string-pulling behavior, with no rats requiring overnight training. All animals required on average two days of shaping to consistently retrieve cashews on all eight trials. As is illustrated in Fig. 2 panel C, high level of grasp accuracy was observed throughout testing and rats required six to nine grasps to retrieve the cashew from the 150 cm string. On average the rats made 67 string contacts per day associated with an average of 3 misses (the hand did not successfully grasp the string on an attempted grasp). An ANOVA conducted on success did not reveal a significant effect of forelimb [$F(1,4) = 2.155, p = 0.216, \eta_p^2 = 0.350$], day [$F(3,12) = 2.067, p = 0.158, \eta_p^2 = 0.341$], nor Forelimb \times Day interaction [$F(23,12) = 1.774, p = 0.205, \eta_p^2 = 0.307$]. In contrast, differences were observed in the distance each forelimb traveled during a trial (Fig. 2 panel D). The ANOVA conducted on average distance traveled per trial revealed a significant effect of day [$F(3,12) = 6.840, p = 0.006, \eta_p^2 = 0.631$]; however, neither the effect of Distance [$F(1,4) = 1.230, p = 0.330, \eta_p^2 = 0.235$] nor the Distance \times Day interaction [$F(3,12) = 1.761, p = 0.208, \eta_p^2 = 0.306$] were significant. A post hoc trend analysis [$F(1,4) = 10.019, p = 0.034, \eta_p^2 = 0.715$] revealed the average distance traveled significantly decreased across days. No differences in distance traveled were observed between forelimbs.

3.2. Bimanual coordination

String-pulling consisted of a number of alternating movements by the forelimbs in which the string was grasped and pulled by one hand and then grasped and pulled by the other. This alteration between limbs was visualized as the continuous change of each forelimb in the y-axis (see panel A of Fig. 3). Direction of movement was represented by calculating the distance moved between each frame (see panel B of Fig. 3). Positive and negative values were associated with downward and upward movements, respectively. All pairs of left and right distances were plotted for the three sample string-pulling trials within a day (see panel C of Fig. 3). A significant inverse relationship was observed between the distances moved by each limb. This relationship was quantified by calculating the correlational between a rat's set of distances and examined changes across days (see panel D of Fig. 3). Although a significant change in correlation was not observed across days [$F(3,12) = 2.558, p = .104, \eta_p^2 = 0.390$], rat average daily correlations were observed to significantly differ from zero on day 3 [$T(4) = 10.288, p = 0.001, d = 4.601$], day 7 [$T(4) = 7.327, p = 0.002, d = 3.277$], and day 14 [$T(4) = 6.198, p = 0.003, d = 2.771$]. Significantly strong bimanual coordination of movement phases was only observed on the last three days of testing.

3.3. Hand shapes and phases of movement

Fig. 4 illustrates the various hand shapes that were associated with a reach and withdraw cycle. Although the movements could vary in terms of the length of reach and withdraw, nearly every reach featured: collect, in which the digits were closed and flexed in preparation for directing the hand toward the string; overgrasp, in which the digits were opened and extended in preparation to grasp; and a purchase that grabbed the string and held the string through the pulling and pushing movements by which the string was reeled in. Once the string was grasped, the hand flexed at the wrist, first to pull the string toward a rat's center of mass, and then extended to push the string further caudally before opening the hand to release the string.

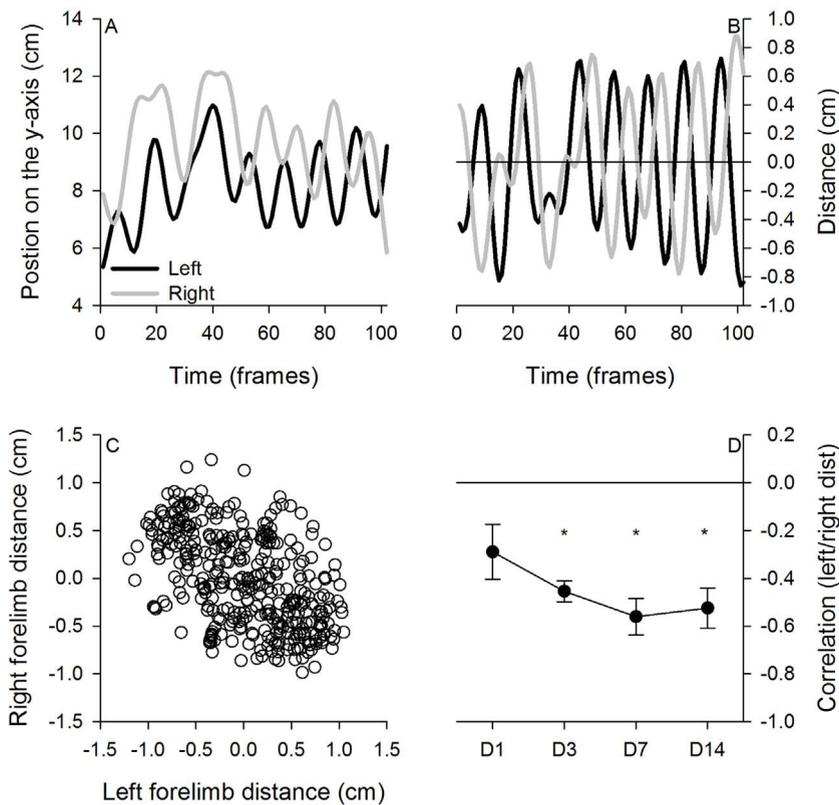


Fig. 3. Position (panel A) and distance (panel B) moved within the y-axes are plotted for both forelimbs during a representative trial. The pairs of distances moved are plotted for all three sample trials for one day (panel C). Average correlations between left and right forelimb distances are plotted for each testing day (panel D).

Fig. 5 plots the topographical representation of a reach, grasp, and withdraw movement that comprised a single cycle of string-pulling for one limb. Labels indicate actions that moved the limb. The dots indicate the location of the hand on successive video frames (30 f/s) and the lines indicate the distance the hand moved. The sequence illustrated in Fig. 5 is relatively large in which the reach phase nearly fully extended the forelimb upward and the withdraw cycle nearly fully extended the forelimb downward. Sequences did vary in excursion lengths. The interframe distances also indicate the higher speed of larger movements (see kinematic results). The details of the movement sequence are summarized in terms of 6 actions. Each action is characterized by the changes in the related forelimb segments that moved the limb, especially between the lower and upper forelimb and by hand shape changes. The major features of a reach are summarized as components of movements that comprised a reach and withdraw cycle are described in Table 1 and are summarized below:

1. *Aim.* The aim is the position of the forelimb/hand just before the hand is advanced toward the string. During an aim the lower arm is held in a vertical orientation, with the hand at the level of the shoulder, aligned with the vertical posture of the trunk and aligned with the side of the trunk. To obtain the aim posture, the hand is lifted, closing at the elbow, by flexing the lower arm in



Fig. 4. Hand shaping movements and their location displayed in a single string-pulling cycle by the right forelimb.

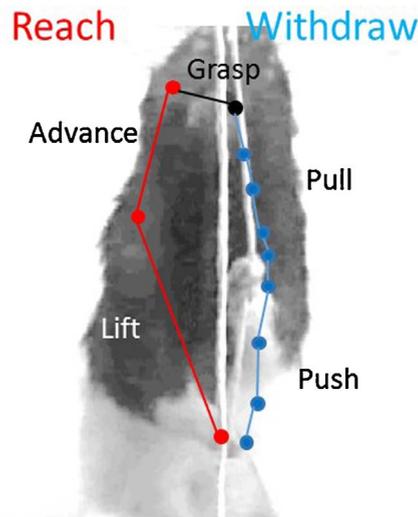


Fig. 5. Frame-by-frame representation of a single string-pulling cycle by the right forelimb. There are two phases of the movement, reach and withdraw. Each phase is characterized by submovements; for the reach, lift and advance and for withdraw grasp, pull and push.

Table 1
Arm movements and Hand movements used for String-Pulling.

	Arm Movements	Hand Movements
1	Aim – elbow closed	Collect – digits lightly flexed and closed
2	Advance – elbow open	Overgrasp – digits extend and open
3	Grasp – elbow open	Purchase – digits close, flex on target
4	Pull – elbow close	Flex – hand flexes at the wrist
5	Push – elbow open	Extend – hand extends at the wrist
6	Release – elbow open	Open – digits extend
7	Lift – elbow close	Digits – flex close

relation to the upper arm. As the hand is brought to the aim position, the digits are lightly closed and flexed in a collect configuration.

2. *Advance*. The advance is produced by both raising the upper arm at the shoulder with a slight adduct movement and then by extending the lower arm by opening at the elbow so that the hand extended upward and toward the midline of the body (the typical location of the string). Toward the end of the advance the digits are both extended and opened so that the hand displayed an overgrasp featuring a completely open hand configuration that anticipated grasping the string.
3. *Grasp*. To perform the grasp, the arm is directed medially with respect to the body by a movement of the upper arm, with some accompanying upper body movement that adducts the elbow, directing the hand medially toward the string. As the open hand contacts the string, the digits are closed and flexed so that the string is grasped. The movement carries the hand and the string medially and somewhat ventrally relative to the upward movement of the advance. As the string is grasped, the hand extends at the wrist and the elbow is slightly adducted to orient the lower arm in a position that is aligned and approximated the body midline.
4. *Pull*. The upper arm is slightly lowered at the shoulder and the lower arm is slightly flexed by closing at the elbow so that the hand grasping the string is lowered in an orientation aligned with the midline of the body. The pull brings the hand to a position at about the middle of the chest, the rat’s center of mass.
5. *Push*. The upper arm continues to be lowered and the lower arm extends by opening at the elbow so that the hand grasping the string is pushed below the thorax, sometimes as low as the ventral belly. For the push the hand begins to extend at the wrist.
6. *Release*. With the hand in an extended and relatively ventral position, the string is released by digit extension accompanied by slight digit opening.

3.4. Reach vs. withdraw movement topography

Motion capture software confirmed that reach and withdraw phases were mainly movements in a vertical orientation and the grasp was mainly in the horizontal orientation (see Fig. 6). Therefore movement within the y-axis was used to segment behavior into reach and withdraw phases. Several measures were used to characterize the topography of each phase across testing days. First, forelimbs travel rather non-circuitous paths through manipulatory space during advance and withdraw phases (see panel A of Fig. 7). The ANOVA conducted on average path circuitry failed to reveal a significant effect of phase [$F(1,4) = 0.701, p = 0.450$,

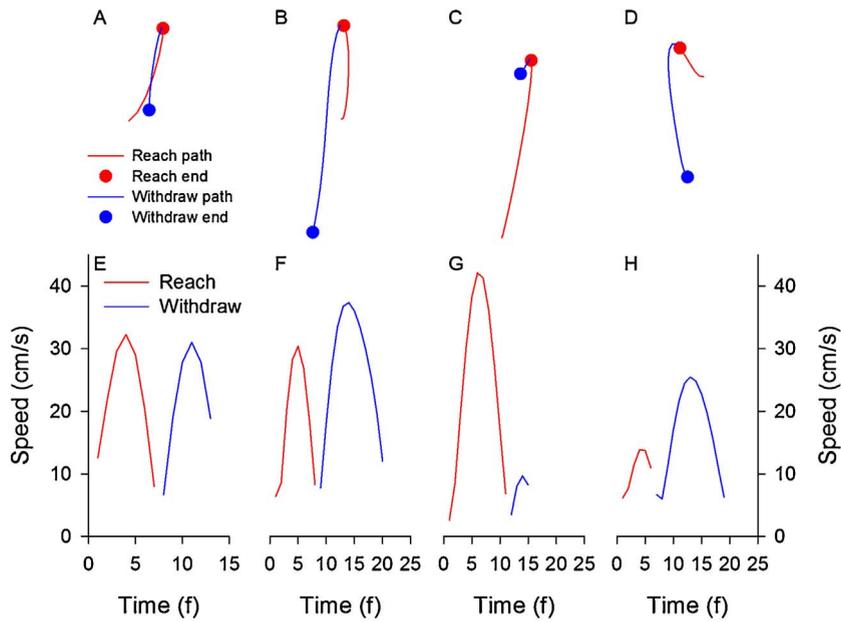


Fig. 6. Topographic (A–D) and kinematic (E–H) profiles are provide from four successive reaching (red lines) and withdraw (blue lines) cycles from one forelimb. The end of each reach (red circle) and withdraw (blue circle) phase is indicated along the path the forelimb follows through manipulatory space. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

$\eta_p^2 = 0.149$], day [F(3,12) = 1.793, $p = 0.202$, $\eta_p^2 = 0.309$], and Phase \times Day interaction [F(3,12) = 0.806, $p = 0.514$, $\eta_p^2 = 0.168$]. Path circuitry did not differ between phases and did not vary as a function of day. Next, the direction of forelimb movements during each phase was highly consistent (see panel B of Fig. 7). The ANOVA conducted on average parameter of concentration failed to reveal a significant effect of phase [F(1,4) = 0.835, $p = 0.413$, $\eta_p^2 = 0.179$], day [F(3,12) = 1.590, $p = 0.243$, $\eta_p^2 = 0.284$], and Phase \times Day interaction [F(3,12) = 1.310, $p = 0.317$, $\eta_p^2 = 0.247$]. The parameter of concentration did not differ between either phase and that did not change across days. Finally, reaching and grasping phases were oriented in opposite directions (see panel C of Fig. 7). The ANOVA conducted on average heading direction revealed a significant effect of phase [F(1,4) = 5745.247, $p < 0.001$, $\eta_p^2 = 0.999$]; however, neither the effect of day [F(3,12) = 2.161, $p = 0.146$, $\eta_p^2 = 0.351$] nor the Phase \times Day interaction were significant [F(3,12) = 1.716, $p = 0.217$, $\eta_p^2 = 0.300$]. Rats were highly consistent in the direction of movement during reaching and grasping phases of string-pulling behavior across days.

3.5. Reach vs. withdraw movement kinematics

Reach and withdraw phases of string-pulling behavior elicit a consistent temporal pacing of moment-to-moment speed (see Fig. 6). In addition, each phase of string-pulling was characterized by peak speeds that were scaled to the Euclidean distance of the movement (see panel A of Fig. 8). Several measures were used to characterize the kinematics of each string-pulling phase across testing days. First, changes in peak speed between phases and across days was investigated (see panel B of Figure). The ANOVA conducted on peak speeds revealed a significant effect of day [F(3,12) = 6.196, $p < 0.01$, $\eta_p^2 = 0.608$]; however, neither phase [F(1,4) = 0.284, $p = 0.622$, $\eta_p^2 = 0.066$] nor Phase \times Day interaction [F(3,12) = 2.007, $p = 0.167$, $\eta_p^2 = 0.334$] were significant. A post hoc linear trend analysis revealed that peak speeds significantly decrease across days [F(1,4) = 10.041, $p < 0.05$, $\eta_p^2 = 0.715$]. Next, differences in reaching and grasping Euclidean distances were examined across days (see panel C of Fig. 8). The ANOVA conducted on Euclidean distance revealed a significant effect of day [F(3,12) = 11.525, $p < 0.01$, $\eta_p^2 = 0.742$] and Phase \times Day interaction [F(3,12) = 4.078, $p < 0.05$, $\eta_p^2 = 0.505$]; however, the main effect of phase [F(1,4) = 0.068, $p = 0.463$, $\eta_p^2 = 0.141$] was not significant. Linear trend analysis revealed a significant decrease in Euclidean distance across days [F(1,4) = 27.804, $p < 0.05$, $\eta_p^2 = 0.874$]; however, Euclidean distance did not differ between phases on any day. Finally, the correlation between peak speeds and Euclidean distances (e.g., movement segmentation) was examined for each phase across testing days (see panel D of Fig. 8). The ANOVA conducted on average movement segmentation failed to reveal a significant effect of phase [F(1,4) = 0.006, $p = 0.944$, $\eta_p^2 = 0.001$], day [F(3,12) = 1.935, $p = 0.178$, $\eta_p^2 = 0.326$], or Phase \times Day interaction [F(3,12) = 0.405, $p = 0.752$, $\eta_p^2 = 0.092$]. Consistent scaling of peak speeds to segment Euclidean distance was observed independent of string-pulling phase or testing day.

4. Discussion

Rats learned to grasp and pull the string to retrieve food using a hand over hand movement. The behavior was acquired within three days of training and was associated with relatively few misses. Topographic features of the reach and withdraw movements

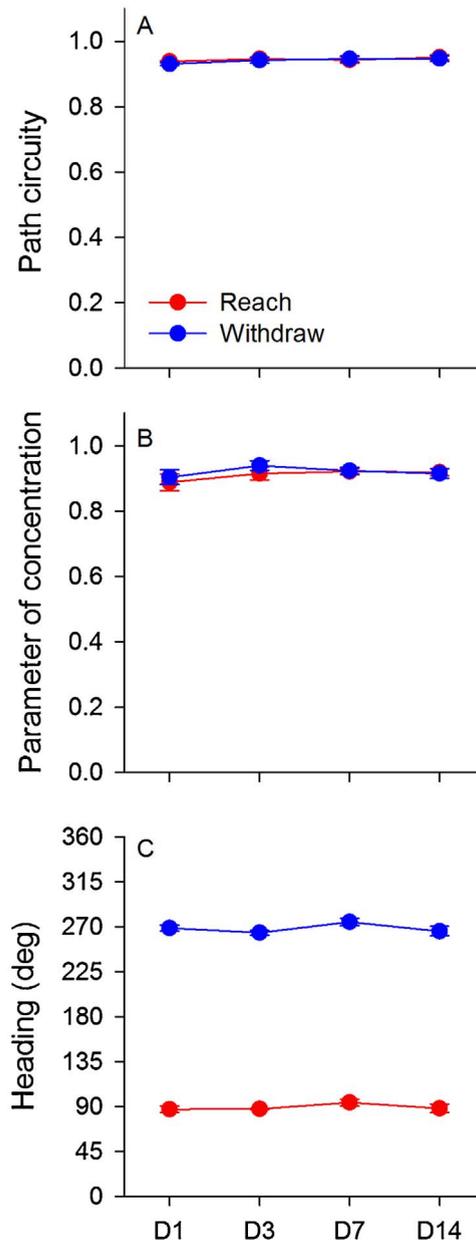


Fig. 7. Average path circuitry (panel B), parameter of concentration (panel C), heading (panel D) are plotted for each phase across testing days.

were similar across days of testing but the average peak speed and Euclidean distance of reach and withdraw were observed to significantly decrease across testing days, suggesting improved efficiency of movement. String-pulling behavior consisted of a reach that advanced the hand to grasp the string and a withdraw that pulled and pushed the string so that the end containing the food was brought toward the animal. Both the reach and withdraw feature a number of different arm movements and a number of different hand shapes. This analysis of string-pulling shows that it is an organized skilled forelimb act that features both coordinated movement of the hand for advancing the string and metacognitive recognition that the act of pulling will advance the food reward.

Many behavioral tasks have been developed to investigate motor function in rats and a number of these tasks focus on use of the hands (Whishaw & Kolb, 2005). One objective of rat hand use studies is modeling the single-handed prehension of humans (Alaverdashvili & Whishaw, 2008; Miklyeva, Castañeda, & Whishaw, 1994; Whishaw, 2000). Thus, it is relevant to ask whether string-pulling movements, as revealed by the present analyses, have similarities to the movements used for single-handed prehension. Both, pulling in a string and reaching for a food item with one hand share similar components. In both tasks, the rat raised a hand to an aiming position with the hand shaped in a collect posture, digits lightly flexed and closed. In both tasks, as the hand is advanced to the target the digits are extended and opened in an overgrasp. In both tasks the digits are closed to grasp, and as the grasp is completed, the hand is extended by a movement at the wrist. The initial phase of withdraw is also similar in the two tasks, with the

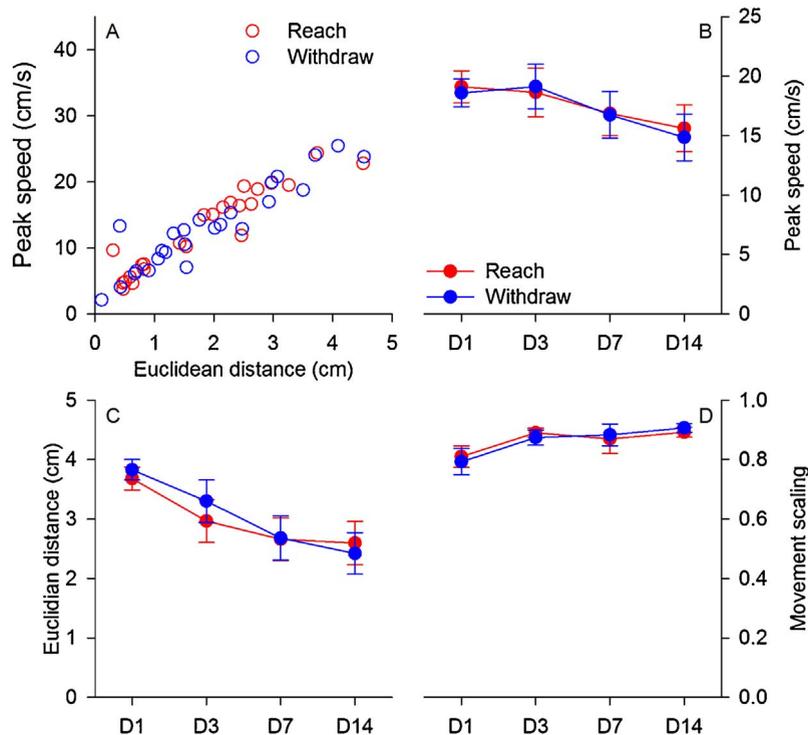


Fig. 8. Peak speed and Euclidean distance pairs are plotted for all reach (red circle) and withdraw (blue circle) phases from a single string-pulling trial (panel A). Average peak speed (panel B), Euclidean distance (panel C), and movement scaling (panel D) are plotted for each phase across testing days. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

hand retracted toward the body. However, there are differences, for in string-pulling the hand pushes the string once a hand brings it to the torso, to further advance it, whereas when reaching for food, the hand brings the food to the mouth. In addition, when reaching for food pellets, a rat sniffs the food to locate it but then lifts the snout away to reach, so that the reach is ballistic. For string-pulling, the reach may be online as the string is always in contact with the snout/vibrissa and for a part of the reach/withdraw, it is also held in the other hand. It is likely that the higher reach success displayed by the rats when string-pulling vs reaching for food is related to the offline vs online sensory control of the movement.

A number of studies using long duration electrical stimulation of motor cortex show that there are two regions of motor cortex that produce forelimb movements, the rostral forelimb area (RFA) and the caudal forelimb area (CRA). Stimulation of the CRA mainly produces arm movements, with advance movements elicited from the rostromedial region of the CRA and withdraw movements elicited from the caudolateral region of the CFA. Stimulation of the RFA produces movements of the hands including digit opening and closing (Brown & Teskey, 2014; Bonazzi et al., 2013; Harrison, Ayling, & Murphy, 2012; Ramanathan, Conner, & Tuszynski, 2006). Therefore, we can suggest that the advance and withdraw of sting-pulling movements are likely associated with activity of the CRA whereas the various digit-shaping movements of string-pulling are associated with RFA. Studies of reaching in primates, including humans, similarly propose that reach and grasp movements are produced by two separate neural channels, a more dorsally located parietofrontal reach channel and a more lateral parietofrontal grasp channel (Jeannerod, 1981, 1999; Karl & Whishaw, 2013). Most human studies, however, limit the analysis of the reach to the advance, from collection to the grasp, and limit hand-shaping analysis to the overgrasp and target purchase. For the rat string-pulling movement, the correlate of the human reach movement would consist of the horizontal movement of the hand that transitions the advance and withdraw and the correlate of the human grasp would be the rat overgrasp and purchase. With respect to the rat string-pulling overgrasp, the hand opening was always maximal, even though the thickness of the string was small. Thus, whereas humans shape their overgrasp in relation to target size, rats apparently do not display a calibrated hand-shape either when reaching for food or reaching for a piece of string. Taken together, from a comparative perspective, rat string-pulling movement is analogous to a human grasp both in terms of movement components and presumptive cortical control.

Movements similar to those displayed for the reach of string-pulling have been observed in the stepping movement of rats walking on a smooth surface, walking across the rungs of a horizontal ladder or reaching up to touch a surface (Whishaw, Travis et al., 2010). For example, in both walking and reaching, the digits are closed and flexed to the collect position at about the midpoint of arm transport, digit opening and extension for an overgrasp occurs just before target contact and withdraw of the hand occurs after hand contact with the target. These movement transitions are also featured in the stepping and reaching movements in other animals including nonhuman primates and humans (Whishaw, Sacrey, Travis, Gholamrezaei, & Karl, 2010). Thus, string-pulling movements of rats feature forelimb movements that appear to be conserved across behaviors and species suggesting that they have a common

evolutionary origin and a common neural basis. Substantial previous work suggested the origin of skilled hand movements is in the step of overground walking (for a review, [Karl & Whishaw, 2013](#)). The ease with which rats display one hand over the other in string-pulling behavior is thus likely attributable to the adaption of the alternating stepping movement of the forelimbs to string-pulling.

A number of features of the string-pulling task suggest that it could be used for investigating the neural basis of skilled forelimb movements and for investigating the neural basis of the recovery from brain injury. First, the string-pulling task can be acquired very quickly, requiring as little as three days of shaping to observe consistent task engagement with high task accuracy. Second, grasp accuracy for string-pulling is high and many successful reaching attempts can be collected in a single training session. Third, string-pulling features similar use of both hands in an alternating pattern, allowing for concurrent contrasts between limb performances in a single session. Fourth, string-pulling is characterized by a great deal of freedom of movement and this freedom could provide insights into the processes of recovery/compensation. Finally, string-pulling can be modified to examine sensory and mnemonic functions. For example, previous work has demonstrated that rats are able to use tactile cues of string size as well as odor cues to guide string-pulling based discrimination learning ([Whishaw & Tomie, 1991](#)). In addition, force (e.g., changing the attached weight) and reinforcement (e.g. changing the length of string) components of the string-pulling task can also be varied.

One caveat must be mentioned with respect to the kinematic measures made in the present study. The digitized results were obtained from a single camera and thus are accurate with respect to the two dimensional features of the reach, grasp, and withdraw movements that were measured. They do not provide an accurate three-dimension representation of movement. Because an animal is nearly always facing in one direction during string-pulling, the present methods could be improved by the use of two cameras and three-dimensional kinematic representations. Digitization was also achieved manually and for future work, markers that facilitate automatic movement tracking could be used. Finally, in the present study, only the movement of the hand was tracked, but because different phases of the reach/withdraw movement involve changes in the relations between limb segments and limb and body segments, a more complete analysis of string-pulling could include digitization of other body parts.

In addition to providing insights into the use of individual limbs in string-pulling, the task has interesting cognitive dimensions in that animals' must have an expectancy with respect to the outcome of the act – a food reward. An animal's repertoire of spatial behaviors has been argued to occur at distinct scales of movement ([Montello, 1993](#)). For example, movement that involves displacement of a limb through an environment would represent a figural or manipulatory scale. In contrast, environmental or ambulatory scale involves movement of the entire body. Different representational systems have been posited to mediate performance at each scale ([Presson, DeLange, & Hazelrigg, 1989](#)). Behavioral and electrophysiological work has provided evidence that similar representational systems encode movement at both scales. Debate has focused on the nature of the representation that mediates movement at the ambulatory scale. One line of research is guided by the view that animals encode a Cartesian map of the environment ([Tolman, 1948](#); see also [O'Keefe & Nadel, 1978](#)), which is supported by the discovery of hippocampal place cells that are firing characteristics tuned to the rat's position in the environment. Other research supports a role for a directional vector or polar coordinate representational system in accounting for a range of spatial behaviors ([Blodgett, McCutchan, & Mathews, 1949](#); [Hamilton, Akers, Weisend, & Sutherland, 2007](#); [Skinner et al., 2003](#)). This directional vector is further supported by the discovery of head direction cells in a network of brain structures that are tuned to rat's directional heading ([Calton et al., 2003](#); [Stackman, Clark, & Taube, 2002](#); [Taube, Muller, & Ranck, 1990](#); [Taube, Kesslak, & Cotman, 1992](#)) and that CA1 cell activity is tuned to spatial distance ([Kjelstrup et al., 2008](#)). Considering the view that the manipulatory scale neural system evolved from brain structures that mediate ambulatory scale movement ([Grillner & Wallen, 1985](#); [Iwaniuk & Whishaw, 2000](#); [Karl & Whishaw, 2013](#)), it is possible a directional vector is used to encode manipulatory scale movement during string-pulling behavior.

Several lines of evidence suggested manipulatory scale representations encode direction and distance of movement. First, performance in manipulatory spatial tasks closely parallels ambulatory scale research supporting the role for directional vector representation. For example, human participants quickly learn the position of Velcro tape hidden on bottom of a shallow well of beads ([Köppen et al., 2013](#)). Second, human participants elicit manipulatory scale movement kinematics that systemically vary as a function of the distance moved ([Gordon, Ghilardi, Cooper et al., 1994](#)). Specifically, non-circuitous segments of movement are associated with moment-to-moment speeds that monotonically increase to a peak speed (typically located at the mid-point of the segment) and then monotonically decrease. Increases in the length of the movement are associated with increases in the peak speed. The results of the current study are consistent with a conservation of this representational system in rat manipulatory scale movement. Specifically, rats exhibited consistent directed movements during each phase of string-pulling. In addition, this consistency in directed movement was observed on the first day of training and did not vary across days. The topographical organization of rat string-pulling behavior is consistent with a representational system encoding ([Wallace et al., 2006](#)). Future work is needed to examine whether a similar network of brain structures mediate this topographical organization.

5. Conclusion

String-pulling is an ethologically relevant behavior that provides an assessment of fine motor control of both forelimbs. Movements of forelimbs can be segmented into a sequence of reaching, grasping and withdrawal phases. Each phase provides an assessment of direction and distance estimation at the rat manipulatory scale. Further work is needed to characterize the network of structures that supports these aspects of movement organization. Topographic and kinematic features of string-pulling behavior may prove a useful tool in characterizing the movement deficits associated with rodent models of neurological pathology and assessing the efficacy of novel therapeutic interventions.

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