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Unilateral forelimb sensorimotor cortex devascularization disrupts the topographic and kinematic characteristics of hand movements while string-pulling for food in the rat

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ABSTRACT

String-pulling by the rat is a bimanual act, in which an upright animal retrieves a piece of food attached to the end of the string by downward hand-over-hand movements. The present study compared the movements of string-pulling, using topographic and kinematic measures of hand movement, in control rats and rats with unilateral sensorimotor motor cortex lesion produced by removal of the pia matter. In the first week following devascularization, the rhythmicity and accuracy of string-pulling movements decomposed; however, thereafter the rhythm of bilateral alternation was restored. Over 70 days of testing, distance traveled decreased for both hands in the control and lesion groups, suggesting that both groups displayed an increase in string-pulling efficiency. Nevertheless, the lesion group exhibited more missed string contacts with the (contralateral-to-lesion) hand and more grasps in which the string was hooked between the digits with both hands. In addition, an increase in mouth grasps was observed in the lesion group. Motion capture analyses revealed that the lesion group exhibited longer reach and withdraw movements and these movements were longer for the ipsilateral-to-lesion vs contralateral-to-lesion hand. Thus, although rhythmicity of string-pulling behavior recovers after sensorimotor cortex devascularization, the contralateral-to-lesion hand contributed less to string pulling and requires mouth grasps to stabilize the string for grasping. The results are discussed in relation to contemporary theories of the contributions of the forelimb motor cortex to skilled movement and the potential use of string-pulling as a therapy for brain injury.

1. Introduction

String-pulling is a behavioral protocol adapted to a wide range of animal species [47,18,38,29,49,32]. The behavior involves alternating reach, grasp, and withdraw movements by the hands in order to retrieve a food item that is attached to the end of a string. String-pulling behavior has been used to investigate a range of cognitive processes (for a review see [23]), neurobiology of mnemonic function [47,48,30], and social learning [2]. The movement of string-pulling likely falls within the natural repertoire of the rat because it is akin to pulling on nesting material, a food object that an animal wants to retrieve, or a branch that might contain a food item. String-pulling behavior is quickly acquired by the rat and offers a behavior that can be used to investigate the neural control of bimanual hand movements used in performing a skilled task [6].

Although there has been no investigation of the neural organization of string-pulling behavior, it is likely that the alternating rhythm and the reach-grasp-withdraw movements of the forelimbs and hands are dependent upon murid central motor systems that include the forelimb regions of the motor cortex. Electrical or optogenetic stimulation of the caudal forelimb area (CFA) of the motor cortex elicits the independent acts of forelimb advance and retract, similar stimulation of the rostral forelimb area (RFA) elicits hand opening and closing movements [7,10,16,36,37,42]. In addition, in conscious animals, stimulation of motor cortex can elicits alternating forelimb movements [19]. Thus, it seems likely that the act of string-pulling, rather than being dependent upon relatively discrete forelimb regions of one hemisphere, would require coordinated action of all of these forelimb regions and their synchrony by both hemispheres. Although it is documented that lesion to forelimb motor cortex in the rat produce impairments in many

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forelimb skilled movements, including hand placement when walking [34,4,24], using a single hand to reach for food [1,28,46], and coordinating hand use when handling food for eating [20,25,43], there has been no investigation of the contribution of rodent motor cortex to an intrinsically, coordinated bilateral motor act such as string-pulling. What is especially interesting about string-pulling is that the behavior seemingly requires an identical contribution of each forelimb/hand and so offers a within-task way of comparing the contributions of both hands as well as a way of examining their coordination to a skilled motor act.

The present study examined the effects of a lesion model focused on the forelimb region of the sensorimotor cortex on the organization of string-pulling behavior. End point measures of performance as well as the kinematics of the bilaterally coordinated reach and withdraw movements were used for the analyses. Rats received a unilateral lesion produced by pial removal over the forelimb area of sensorimotor cortex and were examined in the string-pulling task [6] over 70 post-lesion days. The aspects of the behavior that were subject to topographic examination included the rhythmicity of the movements and the relative contributions of the contralateral-to-lesion hand, which was expected to be most affected by the devascularization, vs the ipsilateral-to-lesion hand, which was expected to be least affected.

2. Materials and methods

2.1. Animals

Twelve male hooded Long Evans rats were obtained from the Northern Illinois University vivarium at 90 days of age. Rats were housed two to a cage in opaque plastic cages with wire mesh tops. The colony room was maintained at 20–21 °C and on a 12 h light/dark cycle. Throughout behavioral testing rats were food deprived to 85% of their free feeding weight and provided ad libitum access to water. All experimental protocols were approved by the NIU Institutional Animals Care and Use Committee. A subset (first testing block) of the data collected from the control rats has been previous published [6].

2.2. Surgery

Following training, rats received either a lesion produced by removal of the vasculature overlying the sensorimotor cortex (n = 7) or control surgeries (n = 5) focused in the right hemisphere. Rats were anesthetized with a mixture of isoflurane and oxygen. Lesions were made using standard stereotaxic techniques and were visualized with the aid of a surgical microscope. The skin over the skull was opened to expose the surface of the skull. Two holes were made 1.0 mm anterior to bregma at 1.5 mm and 4.5 mm lateral to bregma; two holes were made 4.0 mm posterior to bregma at 1.5 mm and 4.5 mm lateral to bregma [34]. A fine dental burr was used to connect the trephinations creating a rectangular window. Removal of the window and overlying dura mater exposed the sensorimotor cortex associated with the forelimb area [36,37]. Devascularization of the sensorimotor cortex was produced by using a saline moistened cotton swab to wipe away the pia mater and blood vessels. After suturing the surrounding skin with silk, rats were left to recover overnight. Sham rats experienced the same surgical procedures; however, the skull window was not removed and the sensorimotor cortex was not devascularized.

2.3. Apparatus

The string-pulling apparatus was a transparent rectangular cage (46 cm x 26 cm x 26 cm) with a wire mesh top and an opaque barrier restricting access to half of the apparatus. The apparatus was positioned on a table (1.5 m above the floor) in a small room. The string (0.2 cm in dimeter) was 100% cotton that increased in length from training (100 cm) to testing (150 cm). A medium washer was attached to the end of the string in the cage, preventing the string from falling out of the cage when the cashew was attached.

A JVC HD video camera (Model #: GY-HM100U) was positioned perpendicular to the wall of the apparatus with the string. Videos were filmed at 30 frames per second with 1/1000 shutter speed and were stored on DVDs for offline analysis.

2.4. Procedures

Prior to behavior testing, rats were exposed to a cashews in their home cage to avoid neophobic response. Rats were shaped to pull strings to retrieve a cashew attached at the end. During the first day of training, rats were placed in the sting pulling apparatus (without the barrier) with 20 strings of varying length (30 cm–100 cm) baited with cashews (approximately 100 mg). Rats were removed from the apparatus once all of the cashews were retrieved or an hour had elapsed. The following day, rats were put in the string puling apparatus (with the barrier dividing the cage in half) and received eight trials with a 100 cm string. A trial started when the rat was placed in the apparatus and ended after the cashew was retrieved or five minutes had elapsed. Once the cashew was consumed, the rat was removed from the testing apparatus and placed in the holding cage while the apparatus was prepared for the next trial (e.g., cleaning the apparatus, re-baiting the strings). The length of the string was increased to 150 cm the day after a rat retrieved a cashew from all eight trials. Rats were assigned to control or lesion groups after successfully retrieving a cashew on all eight trials across two consecutive days.

Subsequent to surgery, rats were tested one day, three days, and seven days after surgery to characterize initial changes in string pulling behavior. Thereafter rats were tested once a week until 10 weeks post lesion, providing as snapshot of string pulling behavior over time. Testing sessions involved eight trials in which the rat would retrieve a cashew after pulling a 150 cm string.

2.5. Analysis

2.5.1. Motivational analysis of string pulling

Two measures were used as a general assessment of motivation to engage in string pulling behavior. First, approach time was defined as the time elapsed between placement in the apparatus and first contact with the string. Next, pull time was defined as the time elapsed between first string contact and retrieval of the food item.

2.5.2. End point measures

Performance during the string-pulling task depends on contacting and purchasing the string. The following measures were developed to characterize performance. First, percent right hand contacts involved calculating the percentage of right contacts (closure of digits around the string) relative to total number of right and left hand contacts during a trial. Next, percent mouth contacts involved counting the total number of mouth contacts (closure of mouth on the string) and calculating the percent relative to all contacts (right, left, and mouth). Further, misses were defined as a transition between reach and withdraw phases without contacting the string. Finally, hooks were defined as a string contact with the hand that involved the string passing between first-second, second-third, or third-fourth digits. Each of these measures was recorded for trial two, five, and eight within a day and averaged across blocks of three days.

2.5.3. Kinematic analysis

Peak performance motion captured software (Vicon, Denver, CO, USA) was used to capture a subset [2,5,8] of string-pulling trials. During a sample trial, the position of both hands was digitized at 30 frames per second. The resulting x- and y-coordinates were used to characterize topographic and kinematic organization of string-pulling behavior.

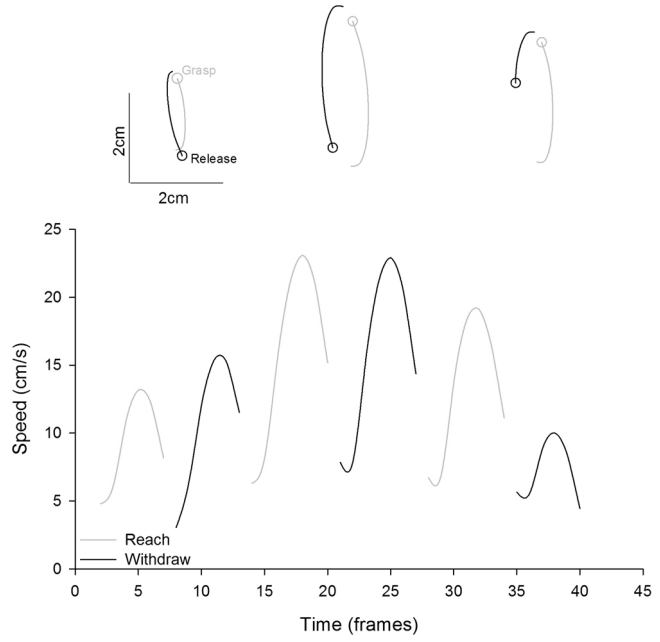

Fig. 1. Topographic (top) and kinematic (bottom) characteristics are plotted for three contiguous string-pulling cycles. Grey lines represent the reach trajectories and black lines represent withdraw trajectories. The grey circle indicates the location of the grasp at the end of a reach trajectory and the black circle indicates the location of the release at the end of the withdraw phase. Note: (1) reach and withdraw movements can vary in excursion length, (2) velocity for both movement phases scales with excursion length.

Bimanually coordinated hand movements were quantified by calculating the moment-to-moment change in position (e.g., distance) as each hand moved within the y-axis [6]. A correlation coefficient was calculated for the set of right and left hand values from the sampled trials within a day. Hands consistently moving in opposite directions would have correlation coefficients approaching −1.0. In contrast, hands consistently moving in the same direction would have correlation coefficients approaching 1.0. Daily correlation coefficients were average across blocks of three days.

The total distance each hand moved was recorded for each of the sample trials and averaged across blocks of three days.

2.5.4. Reach and withdraw component analysis

Each hand cycles through two functionally distinct phases of movement (see Fig. 1). The reach phase involves an upward vertical movement of the hand that occurred between a hand's release of the string and its subsequent string purchase. Each reach phase was normalized such that the origin of movement was defined as the point the hand released the string. The withdraw phase involves a downward vertical movement of the hand while maintaining contact with the string. Each withdraw phase was normalized such that the origin of movement was defined as the point the hand contacted the string. Several measures were used to characterize the topographic and kinematic organization of each phase of movement:

2.5.4.1. Distance. The distance the hand traveled was recorded for each reach and withdraw phase during the three trials. The resulting values were used to calculate a daily average distance moved during each phase.

2.5.4.2. Path circuity. The path circuity of a movement phase was calculated by dividing the Euclidean distance by the total distance traveled for each reach and withdraw phase during the three trials. Path circuity values range from 0.0 to 1.0, with hands following more direct paths through manipulatory space as the ratio approaches 1.0. The resulting values were used to calculate a daily average path circuity for each phase.

2.5.4.3. Parameter of concentration. Reach and withdraw phases of movement involve moving the hand along trajectories through manipulatory space. Circular statistics [5] were used to quantify the consistency of heading directions for each set of reach and withdraw trajectories for all three trials within a day. The start and end coordinates for both phases of movement were transformed such that the start of the path was the origin (0,0) and the angle of the end coordinate was calculated relative to a polar coordinate system (0°: right, 90°: up, 180°: left, 270°: down). The parameter of concentration quantifies the variability in a set of headings with values ranging from 0.0 (variable headings that are uniformly distributed all directions) to 1.0 (no variability in heading). The resulting values were used to calculate average parameter of concentration for each phase across testing blocks.

2.5.4.4. Peak speed. The peak speed hands traveled was recorded for each reach and withdraw phase during the three trials. The resulting values were used to calculate the daily average peak speeds for each phase.

2.5.4.5. Movement scaling. Previous work has shown that rats scale peak speeds of a movement to the Euclidean distance [6]. Specifically, increases in Euclidean distances are associated with faster peak speeds. In the current study, movement scaling was quantified as the correlation coefficient observed between the set of peak speeds and Euclidean distances for each phase of movement within a day. The resulting values were used to calculate the daily average movement scaling for reach and withdraw phases.

2.5.5. Statistical analysis

All statistical analyses included the repeated measure block that reflected four blocks of three days (Block 1: Days 1,3, 7; Block 2: Days 14, 21, 28; Block 3: Day 35, 42, 49; Block 4: Day 56, 73, 70). Several analyses included the repeated measure Hands, designated as left (contralateral-to-lesion) and right (ipsilateral-to-lesion). Repeated measures ANOVAs were used to evaluate main effects and interactions on each dependent measure. The Geenhouse-Geisser (G-G) correction was used in analyses where Mauchly's test indicated significant departure from the assumption of sphericity. Partial eta squared (η^2p) was used as a measure of effect size for each main effect and interaction. Linear trend and Tukey HSD tests were used for post hoc analyses.

2.6. Histology

After behavioral testing, rats were deeply anesthetized and perfused with phosphate-buffered saline, followed by 4% paraformaldehyde. Brains were stored in paraformaldehyde solution for 24 h, and then moved to a 30% sucrose solution for approximately 48 h. The brains were sliced into 40 μm sections using a cryostat, and stained with cresyl violet.

3. Results

3.1. Histology

Due to tissue preparation related issues, histological analysis of lesion extent was only possible for a subset of lesion cases (n = 5). Nevertheless, visual inspection of the brains at removal indicated that all animals hand similar lesions to motor cortex. In the histologically observed cases, the lesions affected the forelimb sensorimotor cortex, as intended, with limited white matter involvement (see Fig. 2). No tissue damage was observed in control rats.

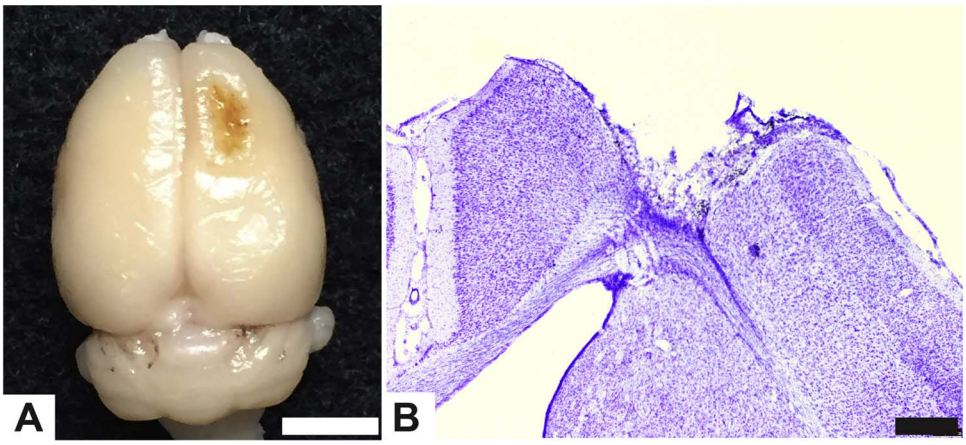

Fig. 2. A full brain picture is provided for a representative rat in the lesion group (scale bar: 5 mm). A coronal section stained with cresyl violet is provided for the same rat to indicate typical depth of lesion extent (scale bar: 500 μm). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. Post-lesion motivational analysis of string pulling

Prior to lesion, rats quickly acquired the string-pulling task and all rats could pull all eight strings by the second day of training. Following the lesion, rats quickly reengaged in string-pulling behavior on the first day of testing. Although both control and lesion groups were equally motivated to engage in string-pulling behavior subsequent to surgery, the lesion group required more time to retrieve the cashew relative to the control group on block 1 (see Fig. 3).

3.2.1. Approach time

There were no differences in approaching and initiating string-pulling by the control group vs the lesion group and both groups made increasingly faster approaches over test blocks. The ANOVA (G-G, $\varepsilon = 0.336$) applied to approach time revealed a significant main effect of block [$F(1.009,10.089) = 7.224$, $p = 0.022$, $\eta_p^2 = 0.419$]; however, neither the main effect of group [$F(1,10) = 2.428$, $p = 0.150$, $\eta_p^2 = 0.195$] nor the Group x Block [$F(1.009,10.089) = 2.217$, $p = 0.167$, $\eta_p^2 = 0.181$] interaction were significant. Post hoc analysis revealed a significant decreasing linear trend in approach time across blocks [$F(1,10) = 7.611$, $p = 0.020$, $\eta_p^2 = 0.432$].

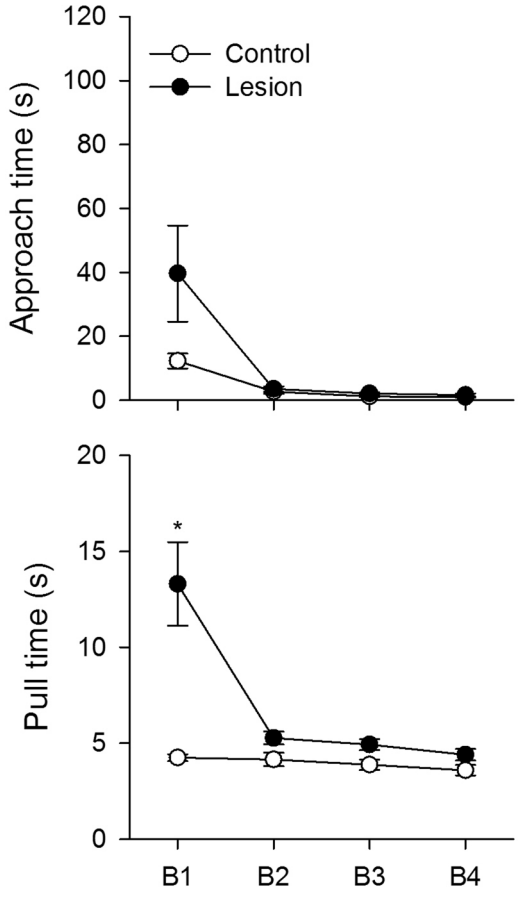

Fig. 3. Each group's average approach (top panel) and pull (bottom panel) are plotted for each testing block (*$p < 0.05$).

3.2.2. Pull time

The lesion group displayed longer pull times in the first post-lesion test block, but thereafter did not differ from the control group. The ANOVA (G-G, $\varepsilon = 0.350$) applied to pull time revealed a significant effect of group [$F(1,10) = 17.174$, $p = 0.002$, $\eta_p^2 = 0.632$], block [$F(1.050,10.495) = 11.093$, $p = 0.007$, $\eta_p^2 = 0.526$], and Group x Block interaction [$F(1.050,10.495) = 9.122$, $p = 0.012$, $\eta_p^2 = 0.477$]. Post hoc analysis revealed a significant decreasing linear trend in pull time across blocks [$F(1,10) = 13.577$, $p = 0.004$, $\eta_p^2 = 0.576$]. Post hoc analysis revealed that groups only significantly differed on the first block of testing (Tukey HSD, $p < 0.05$).

3.3. End point measures

3.3.1. Contacts

Rats that received lesions exhibited a significant increase in the ipsilateral-to-lesion hand contacts in the first block but thereafter did not differ from the control contralateral-to-lesion hand (see top panel of Fig. 4). The ANOVA (G-G, $\varepsilon = 0.370$) conducted on percent ipsilateral-to-lesion contacts revealed a significant effect of group [$F(1,10) = 9.809$, $p = 0.011$, $\eta_p^2 = 0.495$], block [$F(1.110, 11.095) = 6.998$, $p = 0.021$, $\eta_p^2 = 0.412$], and Group x Block interaction [$F(1.110,11.095) = 6.951$, $p = 0.021$, $\eta_p^2 = 0.410$]. Post hoc analysis revealed a significant decreasing linear trend in percent ipsilateral-to-lesion contacts across blocks [$F(1,10) = 10.173$, $p = 0.010$, $\eta_p^2 = 0.504$]. In addition, groups only significantly differed on the first block of testing (Tukey HSD, $p < 0.05$).

In addition, lesion rats exhibited a significantly higher percent mouth contacts across all testing blocks (see bottom panel of Fig. 4). The ANOVA conducted on percent mouth contacts revealed a significant effect of group [$F(1,10) = 6.824$, $p = 0.026$, $\eta_p^2 = 0.406$], block [$F(3,30) = 3.660$, $p = 0.023$, $\eta_p^2 = 0.268$], and Group x Block interaction [$F(3,30) = 3.291$, $p = 0.034$, $\eta_p^2 = 0.248$]. Post hoc analysis revealed a significant decreasing linear trend in percent mouth contacts across blocks [$F(1,10) = 5.024$, $p = 0.049$, $\eta_p^2 = 0.334$]. Groups were observed to differ at all blocks of testing (Tukey HSD, $p < 0.05$).

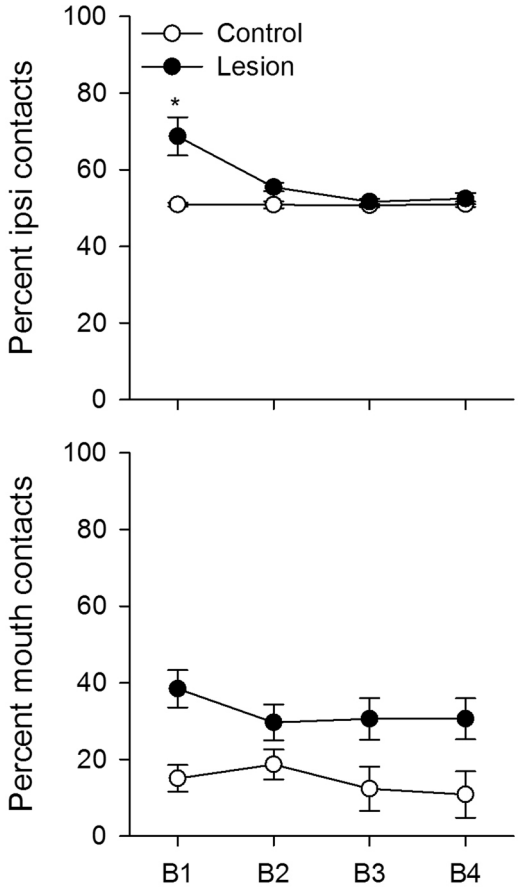

Fig. 4. Each group's average percent right contacts (top panel) and percent mouth contacts (bottom panel) are plotted for each testing block (*p < 0.05).

3.3.2. Misses

Differences in contacting the string were also associated with less accurate pulling behavior (see Fig. 5). The lesion group made significantly more misses with both hands relative to the control group, with the lesion group also exhibiting more misses with the contralateral-to-lesion relative to the ipsilateral-to-lesion hand. The ANOVA (G-G, $\varepsilon = 0.514$) conducted on misses for the contralateral-to-lesion hand revealed a significant effect of group [$F(1,10) = 24.877$, $p = 0.001$, $\eta_p^2 = 0.713$], block [$F(1.541,15.415) = 8.988$, $p = 0.004$, $\eta_p^2 = 0.473$], and Group x Block interaction [$F(1.541,15.415) = 12.966$, $p = 001$, $\eta_p^2 = 0.565$]. Post hoc analyses revealed that the lesion group exhibited significantly more misses across all blocks, except block four (Tukey HSD, $p < 0.05$).

The ANOVA (G-G, $\varepsilon = 0.549$) conducted on misses for the ipsilateral-to-lesion hand revealed a significant effect of group [$F(1,10) = 5.593$, $p = 0.040$, $\eta_p^2 = 0.359$]; however, neither the effect of block [$F(1.244, 12.435) = 1.478$, $p = 0.255$, $\eta_p^2 = 0.129$] nor Group x Block interaction [$F(1.244,12.435) = 0.415$, $p = .0575$, $\eta_p^2 = 0.040$] were significant.

3.3.3. Hooks

A comparison of the number of times that the hand hooked the string between digits (rather than grasping with an open hand) indicted that rats in the lesion group made more hooks with both hands than observed in the control group; however, the increase was only significant for the ipsilateral-to-lesion hand. The ANOVA conducted on hooks for the contralateral-to-lesion hand during the reach phases failed to reveal a significant effect of group [$F(1,10) = 3.063$, $p = 0.111$, $\eta_p^2 = 0.234$], block [$F(1.647,16.472) = 0.757$, $p = 0.460$ $\eta_p^2 = 0.070$], or Group x Block interaction [$F(1.672,16.472) = 1.220$, $p = 0.312$, $\eta_p^2 = 0.109$].

The ANOVA conducted on hooks for the ipsilateral-to-lesion hand during reach phases revealed that more hooks were made by the lesion group, Group [$F(1,10) = 7.773$, $p = 0.019$, $\eta_p^2 = 0.437$]; however, neither the effect of Block [$F(3,30) = 0.367$, $p = 0.777$, $\eta_p^2 = 0.035$] nor Group x Block interaction [$F(3,30) = 0.521$, $p = 0.671$, $\eta_p^2 = 0.050$] were significant.

3.4. Kinematic analysis

3.4.1. Bimanual coordination

A decrease in the synchrony in pulling by both hands was observed in the lesion group, but only in the first block of testing. Varying levels of right and left hand movement synchrony were observed on individual trials during the first block between control (see Fig. 6A) and lesion (see Fig. 6B) groups. Daily movement synchrony values were represented by correlations between the set of distances moved for each hand. Control rats exhibited strong negative correlations (see Fig. 6C); whereas, lesion rats exhibited weaker correlations (see Fig. 6D). These differences in movement synchrony were only observed during the first block and were resolved by subsequent testing blocks (see Fig. 6E).

The ANOVA (G-G, $\varepsilon = 0.449$) conducted on bimanual coordination correlations revealed that the effect of Group [$F(1,10) = 2.703$, $p = 0.131$, $\eta_p^2 = 0.213$] was not significant. There were significant effects of Block [$F(1.347, 13.472) = 7.970$, $p = 0.009$, $\eta_p^2 = 0.444$] and Group x Block [$F(1.347, 13.472) = 4.807$, $p = 0.038$, $\eta_p^2 = 0.325$] interaction, while significant group differences were only observed on the first block of testing (Tukey HSD $p < 0.05$). Post hoc linear trend analysis [$F(1,10) = 19.898$, $p = 0.001$, $\eta_p^2 = 0.666$] revealed decreasing in bimanual coordination correlations across blocks in both control and lesion groups indicating a general increase in synchrony, perhaps due to experience/training.

3.4.2. Total distance

Group differences were observed in the total distance each hand traveled during a trial (see Fig. 7). The contralateral-to-lesion hands of the lesion group traveled longer distances than observed in the control group; however, both groups were observed to have a reduction in contralateral-to-lesion hand travel distance across blocks. The ANOVA (G-G, $\varepsilon = 0.420$) applied to the total distance traveled by the contralateral-to-lesion hand reveled a significant effect of group [$F(1,10) = 6.025$, $p = 0.034$, $\eta_p^2 = 0.376$] and block [$F(1.260,12.597) = 12.158$, $p = 0.003$, $\eta_p^2 = 0.549$]; however, the Group x Block interaction [$F(1.260,12.597) = 2.698$, $p = 0.120$, $\eta_p^2 = 0.212$] was not significant. Post hoc analysis revealed a significant linear trend in contralateral-to-lesion hand travel distance across blocks [$F(1,10) = 17.506$, $p = 0.002$, $\eta_p^2 = 0.636$].

The ipsilateral-to-lesion hands of the lesion group traveled longer distances than observed in the control group. Although a reduction in ipsilateral-to-lesion hand travel distance was observed in both groups, larger group differences were observed on early blocks relative to later blocks. The ANOVA (G-G, $\varepsilon = 0.406$) applied to the total distance traveled by the ipsilateral-to-lesion hand reveled a significant effect of group [$F(1,10) = 12.552$, $p = 0.005$, $\eta_p^2 = 0.557$], block [$F(1.217,12.166) = 18.330$, $p = 0.001$, $\eta_p^2 = 0.647$], and Group x Block interaction [$F(1.217,12.166) = 6.247$, $p = 0.023$, $\eta_p^2 = 0.385$].Post hoc analysis revealed a significant linear trend in ipsilateral-to-lesion hand travel distance across blocks [$F(1,10) = 27.580$, $p < 0.001$, $\eta_p^2 = 0.734$].

3.4.3. Reach component analysis

A set of control and lesion reach trajectories are plotted from early (B1) and late (B4) testing trials (see Fig. 8). The lesion was observed to increase the distance moved by both hands during the reach phase; however, only distances traveled by the ipsilateral-to-lesion hand was significant (see top panels of Fig. 9).

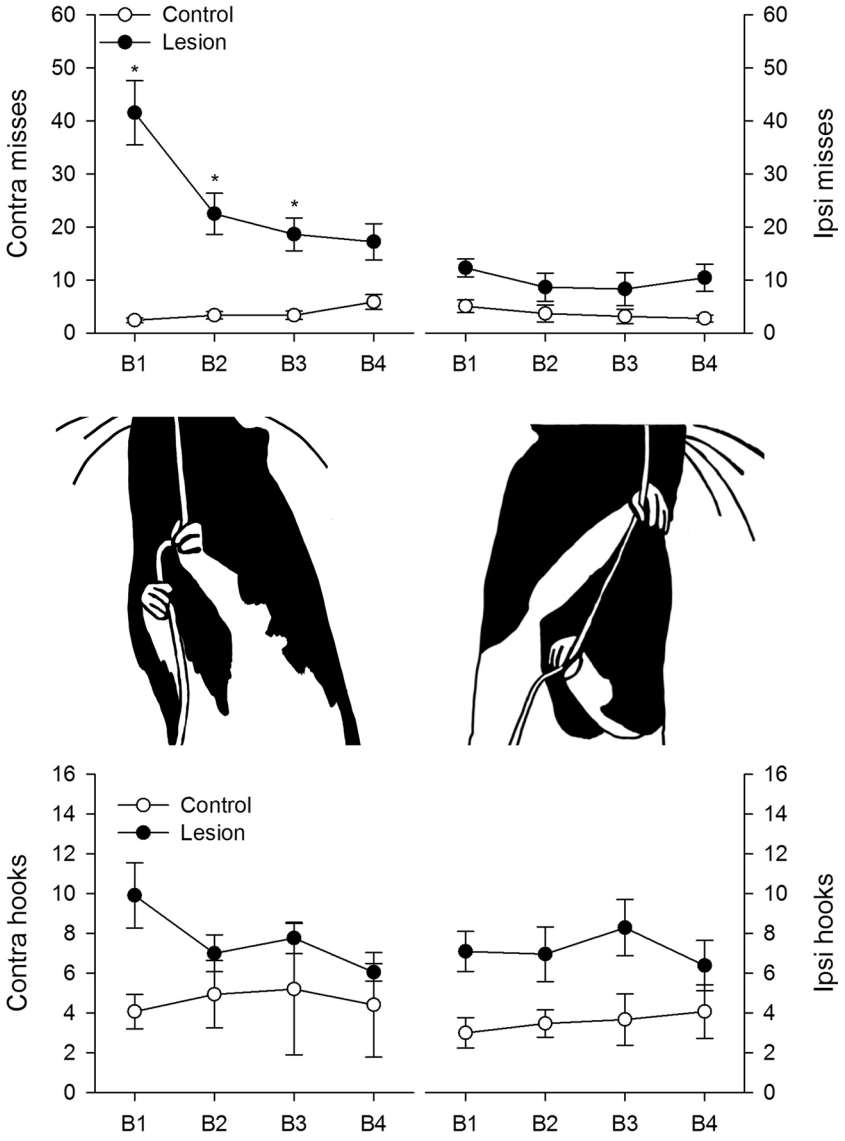

Fig. 5. Average number of misses are plotted for the left (top left panel) and right (top right panel) hands across testing blocks (*p < 0.05). An illustration of a hook is provided for the left (middle left panel) and right (middle right panel) hands. Average number of hooks are plotted for the left (bottom left panel) and right (bottom right panel) hands across testing blocks.

The ANOVA (G-G, $\varepsilon = 0.501$) applied to the distance traveled during the reach phase by the contralateral-to-lesion hand failed to reveal a significant effect of group [$F(1,10) = 2.963$, $p = 0.116$, $\eta_p^2 = 0.229$], block [$F(1.502, 15.018) = 0.995$, $p = 0.370$, $\eta_p^2 = 0.091$], or Group x Block interaction [$F(1.502, 15.018) = 0.420$, $p = 0.608$, $\eta_p^2 = 0.040$]. The ANOVA (G-G, $\varepsilon = 0.501$) applied to the distance traveled by the ipsilateral-to-lesion hand revealed a significant effect of group [$F(1,10) = 7.117$, $p = 0.024$, $\eta_p^2 = 0.416$]; however, neither the main effect of block [$F(1.204, 12.036) = 3.122$, $p = 0.098$, $\eta_p^2 = 0.238$] nor the Group by Block interaction [$F(1.204, 12.036) = 1.047$, $p = 0.342$, $\eta_p^2 = 0.095$] were found to be significant.

Path circuity represent the complexity of the path the hand follows through manipulatory space. Both control and lesion groups exhibited non-circuitous movement during the reach phases that did not change across testing blocks (see middle panels of Fig. 9). The ANOVA applied to path circuity of the contralateral-to-lesion hand during reach phases failed to reveal a significant effect of group [$F(1,10) = 0.342$, $p = 0.572$, $\eta_p^2 = 0.033$], block [$F(3,30) = 0.361$, $p = 0.781$, $\eta_p^2 = 0.035$], or Group x Block interaction [$F(3,30) = 0.565$, $p = 0.642$, $\eta_p^2 = 0.053$]. Similarly, the ANOVA applied to path circuity of the ipsilateral-to-lesion hand during reach phases failed to reveal significant effect of group [$F(1,10) = 0.787$, $p = 0.396$, $\eta_p^2 = 0.073$], block [$F(3,30) = 1.615$, $p = 0.207$, $\eta_p^2 = 0.139$], or Group x Block interaction [$F(3,30) = 1.388$, $p = 0.265$, $\eta_p^2 = 0.122$].

The parameter of concentration provides a measure of heading consistency for a set of trajectories through space. The lesion produced an initial bilateral decrease in the consistency of reach phase headings that significantly increased across subsequent blocks (see bottom panels of Fig. 9). The ANOVA conducted on the parameter of concentration for contralateral-to-lesion hand reach phases reveled a significant effect of block [$F(3,30) = 7.958$, $p < 0.001$, $\eta_p^2 = 0.443$] and Group x Block interaction [$F(3,30) = 8.363$, $p < 0.001$, $\eta_p^2 = 0.455$]; however, the effect of group [$F(1,10) = 0.001$, $p = 0.989$, $\eta_p^2 = 0.000$] was not significant. Linear trend analyses conducted across blocks revealed a significant increase in parameter of concentration across blocks for the lesion group [$F(1,6) = 44.647$, $p = 0.001$, $\eta_p^2 = 0.882$]; however, a significant change across blocks was not observed in the control group [$F(1,4) = 0.023$, $p = 0.887$, $\eta_p^2 = 0.006$]. The ANOVA (G-G, $\varepsilon = 0.542$) conducted on the parameter of concentration for the ipsilateral-to-lesion hand revealed a significant Group x Block interaction [$F(1.625, 16.255) = 5.724$, $p = 0.017$, $\eta_p^2 = 0.364$]; however, neither the effect of group [$F(1,10) = 2.283$, $p = 0.162$, $\eta_p^2 = 0.186$] nor block [$F(1.625, 16.255) = 3.272$, $p = 0.072$, $\eta_p^2 = 0.247$] were significant. Linear trend analyses conducted across blocks revealed a significant increase in parameter of concentration across blocks for the lesion group [$F(1,6) = 12.258$, $p = 0.013$, $\eta_p^2 = 0.671$]; however, a

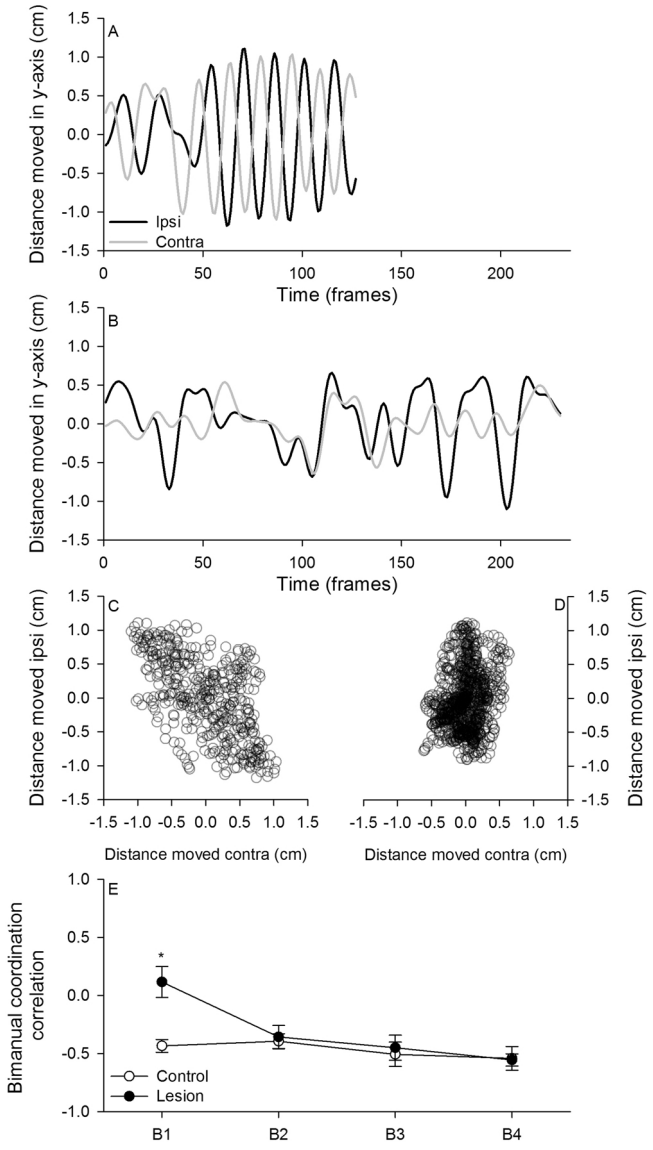

Fig. 6. Distance moved within the y-axis is plotted for both hands from a representative control (panel A) and lesion (panel B) rats during a single-string pulling trial. The distance both hands moved within the y-axis are presented as a scatter plot for representative control (panel C) and lesion (panel D) rats during the sampled trials (3, 5, and 8) for a single day. Average bimanual correlations are plotted for both groups across testing blocks (panel E, *p < 0.05).

significant change across blocks was not observed in the control group [$F(1,4) = 0.152$, $p = 0.717$, $\eta_p^2 = 0.037$].

Rats in both groups were observed to scale peak speeds to the Euclidean distance of the reach phase (see top panels of Fig. 10).

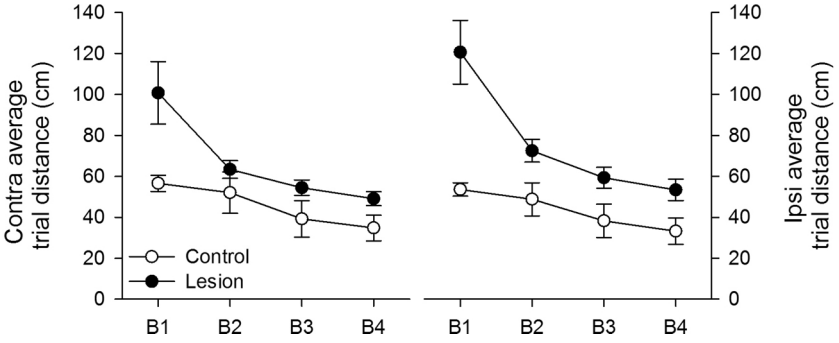

Fig. 7. Each group's average trial distance traveled is plotted for the left (left panel) and right (right panel) hands are across testing blocks.

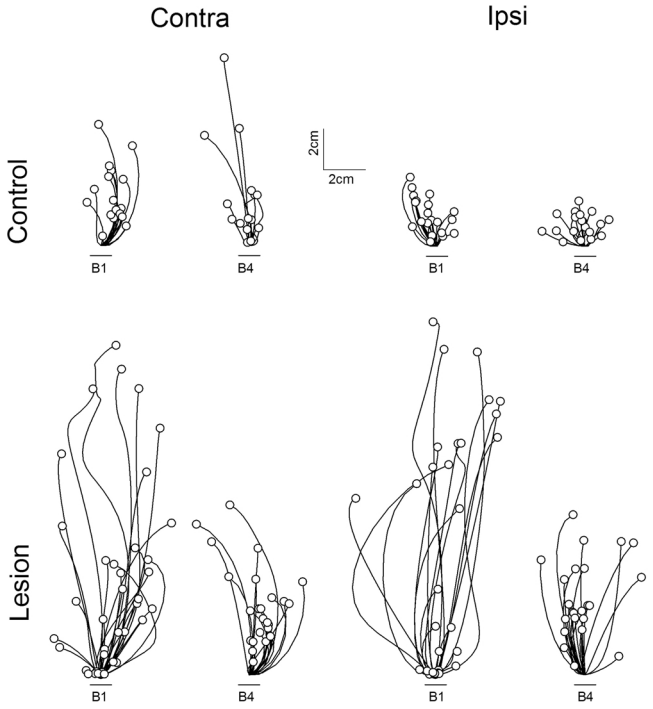

Fig. 8. Representative control (top) and lesion (bottom) reach phase trajectories are plotted for left and right hands from a single trial during block 1 and 4. Note: Start location (midpoint of each horizontal line) was standardized to the origin for all trajectories and the end location is indicated by the open circle.

Although the lesion group exhibited faster reach phase peak speeds relative to the control group, the increase was only significant for the ipsilateral-to-lesion hand (see middle panels of Fig. 10). The ANOVA (G-G, $\varepsilon = 0.562$) conducted on peak reach speeds for the contralateral-to-lesion hand failed to reveal a significant effect of group [$F(1,10) = 0.734$, $p = 0.412$, $\eta_p^2 = 0.068$], block [$F(1.685, 16.855) = 0.437$, $p = 0.728$, $\eta_p^2 = 0.042$], and Group x Block interaction [$F(1.685, 16.855) = 3.620$, $p = 0.056$, $\eta_p^2 = 0.266$]. The ANOVA (G-G, $\varepsilon = 0.445$) conducted on peak speeds for the ipsilateral-to-lesion hand revealed a significant effect of group [$F(1,10) = 6.019$, $p = 0.034$, $\eta_p^2 = 0.376$]; while the main effect of block [$F(1.335, 13.347) = 0.463$, $p = 0.563$, $\eta_p^2 = 0.044$] and Group x Block interaction [$F(1.335, 13.347) = 0.651$, $p = 0.477$, $\eta_p^2 = 0.061$] were not significant.

Movement scaling or the correlation between peak speeds and Euclidean distances for reach phase trajectories, did not vary as a function of group or block (see bottom panels of Fig. 10). The ANOVA (GG, $\varepsilon = 0.482$) conducted on movement scaling for the contralateral-to-lesion hand during reach phases failed to reveal a significant effect of group [$F(1,10) = 0.065$, $p = 0.803$, $\eta_p^2 = 0.006$], block [$F(1.446, 14.464) = 1.736$, $p = 0.212$, $\eta_p^2 = 0.148$], and Group x Block interaction [$F(1.446, 14.464) = 0.058$, $p = 0.981$, $\eta_p^2 = 0.006$]. The ANOVA conducted on movement scaling for the ipsilateral-to-lesion hand

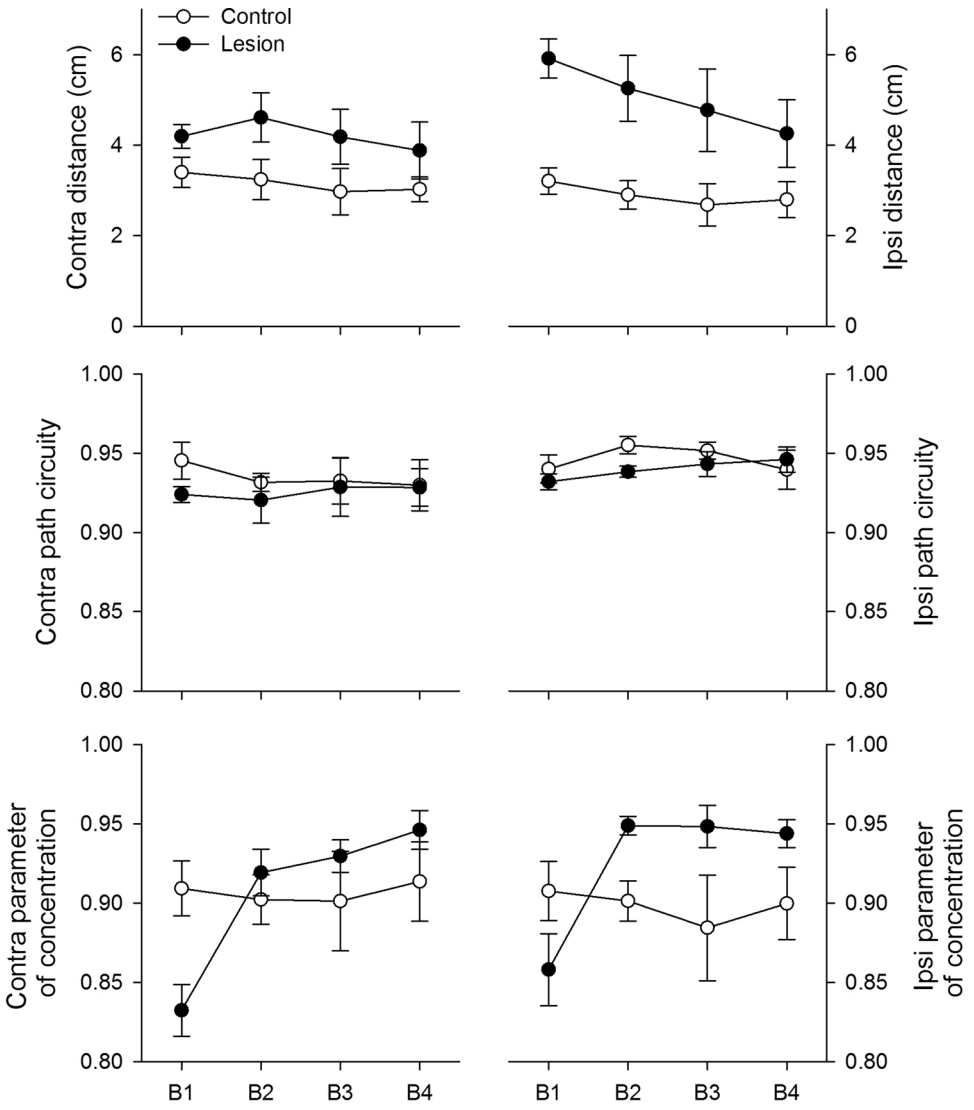

Fig. 9. Average distance traveled for the left (top left) and right (top right) hands during reach phases is plotted for both groups across testing blocks. Average path circuity for the left (middle left) and right (middle right) hands during reach phases is plotted for both groups across testing blocks. Average parameter of concentration for the left (bottom left) and right (bottom right) hands during reach phases is plotted for both groups across testing blocks.

during reach phases failed to reveal a significant effect of group [$F(1,10) = 2.273$, $p = 0.163$, $\eta_p^2 = 0.185$], block [$F(3,30) = 0.041$, $p = 0.989$, $\eta_p^2 = 0.004$], and Group x Block interaction [$F(3,30) = 0.333$, $p = 0.801$, $\eta_p^2 = 0.032$].

3.4.4. Withdraw component analysis

A set of control and lesion withdraw trajectories are plotted from early (B1) and late (B4) testing trials (see Fig. 11). The lesion did not significantly change the distance moved by the contralateral-to-lesion hand. In contrast, significant increases in distance traveled by the ipsilateral-to-lesion hand were observed across testing blocks (see top panel of Fig. 12). The ANOVA (G-G, $\varepsilon = 0.467$) applied to distance traveled by the contralateral-to-lesion hand failed to reveal a significant effect of group [$F(1,10) = 3.395$, $p = 0.95$, $\eta_p^2 = 0.253$], block [$F(1.402, 14.022) = 1.570$, $p = 0.217$, $\eta_p^2 = 0.136$], and Group x Block interaction [$F(1.402,14.022) = 0.994$, $p = 0.409$, $\eta_p^2 = 0.090$]. The ANOVA (G-G, $\varepsilon = 0.408$) applied to distance traveled by the ipsilateral-to-lesion hand revealed a significant effect of group [$F(1,10) = 7.925$, $p = 0.018$, $\eta_p^2 = 0.442$] and block [$F(1.223,12.234) = 5.645$, $p = 0.029$, $\eta_p^2 = 0.361$]; however, the Group x Block interaction [$F(1.223,12.234) = 0.829$, $p = 0.404$, $\eta_p^2 = 0.077$] was not significant. Post hoc linear trend analysis revealed that distance traveled by the ipsilateral-to-lesion hand significantly decreased across blocks [$F(1,10) = 7.385$, $p = 0.022$, $\eta_p^2 = 0.425$].

Path circuity, or the complexity of the path each hand followed through space was recorded for all withdraw phases. Both groups exhibited non-circuitous movement during withdraw phases; however, the lesion produced an acute increase in path complexity in the ipsilateral-to-lesion hand (see middle panels of Fig. 12). The ANOVA applied to path circuity of the contralateral-to-lesion hand during withdraw phases failed to reveal a significant effect of group [$F(1,10) = 1.559$, $p = 0.240$, $\eta_p^2 = 0.135$], block [$F(3,30) = 0.034$, $p = 0.992$, $\eta_p^2 = 0.003$], and Group x Block interaction [$F(3,30) = 0.705$, $p = 0.705$, $\eta_p^2 = 0.045$]. The ANOVA applied to path circuity of the ipsilateral-to-lesion hand during withdraw phases revealed a significant effect of block [$F(3.30) = 4.731$, $p = 0.008$, $\eta_p^2 = 0.321$] and Group x Block interaction [$F(3,30) = 3.950$, $p = 0.017$, $\eta_p^2 = 0.283$]; however, the main effect of group [$F(1,10) = 1.710$, $p = 0.220$, $\eta_p^2 = 0.146$] was not significant. Post hoc linear trend analysis revealed that paths became significantly more direct across testing, block [$F(1,10) = 8.734$, $p = 0.014$, $\eta_p^2 = 0.466$]. Control and lesion groups were only observed to significantly differ in path circuity of the ipsilateral-to-lesion hand on the first testing block (Tukey HSD, $p < 0.05$).

The parameter of concentration provided a measure of heading consistency for a set of withdraw trajectories. The lesion produced an acute increase in heading variability in the contralateral-to-lesion hand that became significantly more concentrated across testing blocks, relative to the control group (see bottom panels of Fig. 12). The ANOVA

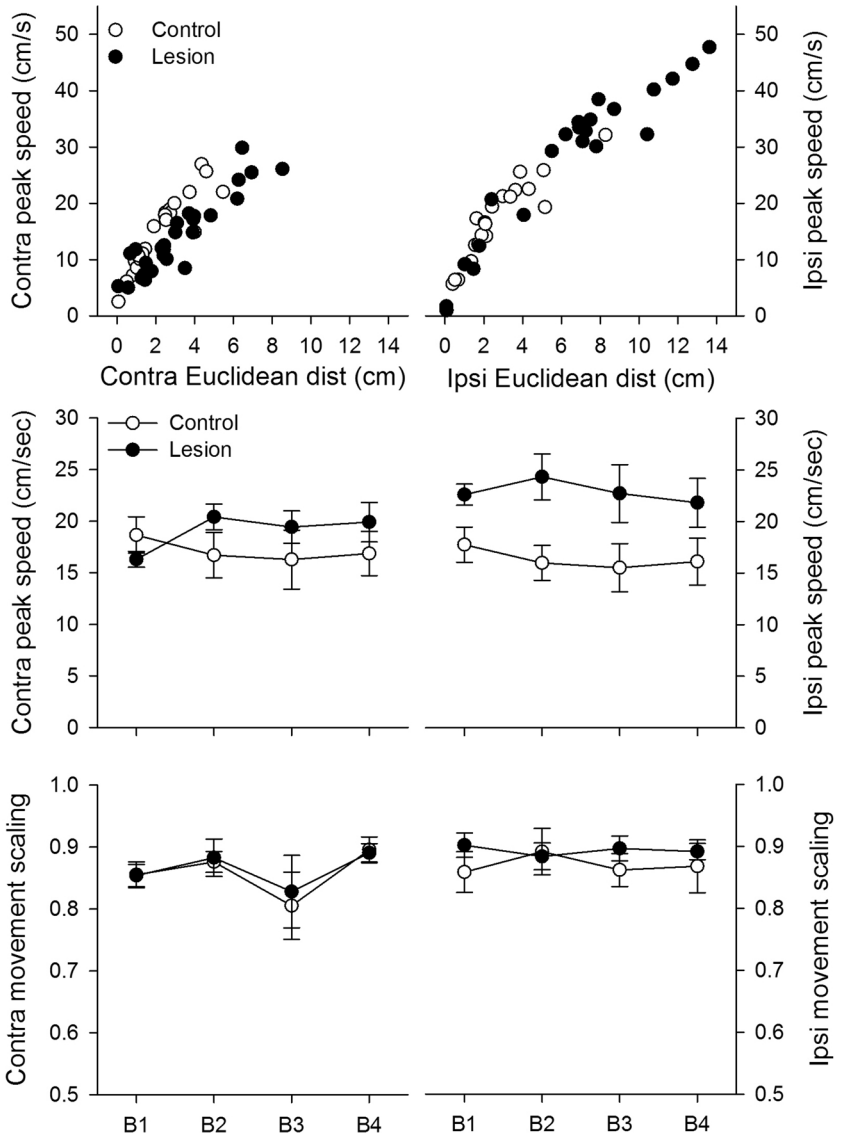

Fig. 10. Peak speeds and Euclidean distances are plotted for all left (top left panel) and right (top right panel) hands reaches within a single string pulling trial. Average peak speed is plotted for the left (middle left panel) and right (middle right panel) hands across testing blocks. Average movement scaling scores during reach phases are plotted for the left (bottom left panel) and right (bottom right panel) hands across testing blocks.

conducted on the parameter of concentration for contralateral-to-lesion hand withdraw phases revealed a significant Group x Block interaction, [$F(3,30) = 6.255$, $p = 0.002$, $\eta_p^2 = 0.385$]; however, neither the main effect of group [$F(1,10) = 0.277$, $p = 0.610$, $\eta_p^2 = 0.0.27$], nor the main effect of block [$F(3,30) = 2.056$, $p = 0.127$, $\eta_p^2 = 0.171$], were significant. Linear trend analyses conducted across blocks failed to reveal a significant increase in parameter of concentration across blocks for the control group [$F(1,4) = 0.478$, $p = 0.527$, $\eta_p^2 = 0.107$]; however, the lesion group [$F(1,6) = 23.842$, $p = 0.003$, $\eta_p^2 = 0.799$] exhibited a significant linear increase across blocks. The ANOVA (G-G, $\varepsilon = 0.510$) conducted on the parameter of concentration for the ipsilateral-to-lesion hand reveled a marginally significant Group x Block interaction [$F(1.529,15.289) = 3.858$, $p = 0.054$, $\eta_p^2 = 0.278$]; however, neither the effect of group [$F(1,10) = 2.925$, $p = 0.118$, $\eta_p^2 = 0.226$] nor the effect of block [$F(1.529,15.289) = 0.847$, $p = 0.479$, $\eta_p^2 = 0.078$] were significant. Linear trend analyses conducted across blocks failed to reveal a significant increase in parameter of concentration across blocks for the control group [$F(1,4) = 0.215$, $p = 0.667$, $\eta_p^2 = 0.051$]; however, the lesion group [$F(1,6) = 7.872$, $p = 0.031$, $\eta_p^2 = 0.567$] exhibited a significant linear increase across blocks.

Rats in both groups were observe to scale peak speeds to the Euclidean distance of the withdraw phase (see top panels of Fig. 13). Although the lesion group exhibited faster reach phase peak speeds relative to the control group, the increase was only significant for the ipsilateral-to-lesion hand (see middle panels of Fig. 13). The ANOVA (G-G, $\varepsilon = 0.528$) conducted on peak speeds for the contralateral-to-lesion hand revealed a significant Group x Block interaction, [$F(1.583,15.825) = 4.634$, $p = 0.033$, $\eta_p^2 = 0.317$]. Neither the main effect of group [$F(1,10) = 0.456$, $p = 0.515$, $\eta_p^2 = 0.044$] nor block [$F(1.583,15.825) = 0.041$, $p = 0.988$, $\eta_p^2 = 0.004$] were significant. Post hoc analysis did not reveal any group differences at any block. The ANOVA (G-G, $\varepsilon = 0.509$) conducted on peak speeds for the ipsilateral-to-lesion hand revealed a significant effect of group, [$F(1,10) = 5.507$, $p = 0.041$, $\eta_p^2 = 0.355$. Neither block [$F(1.528,15.895) = 0.183$, $p = 0.777$, $\eta_p^2 = 0.018$] nor the Group by Block interaction [$F(1.528,15.895) = 3.286$, $p = 0.075$, $\eta_p^2 = 0.247$] were significant.

Movement scaling, or the correlation between peak speeds and Euclidean distances for withdraw phase trajectories, was observed to reduce across both hands; however, significant group differences were selective to the contralateral-to-lesion hand (see bottom panels of Fig. 13). Specifically, the lesion reduced the strength of movement scaling of the contralateral-to-lesion hand. The ANOVA conducted on movement scaling for the contralateral-to-lesion hand revealed a significant effect of group [$F(1,10) = 16.247$, $p = 0.002$, $\eta_p^2 = 0.619$]. Neither the effect of block [$F(3,30) = 0.036$, $p = 0.991$, $\eta_p^2 = 0.004$],

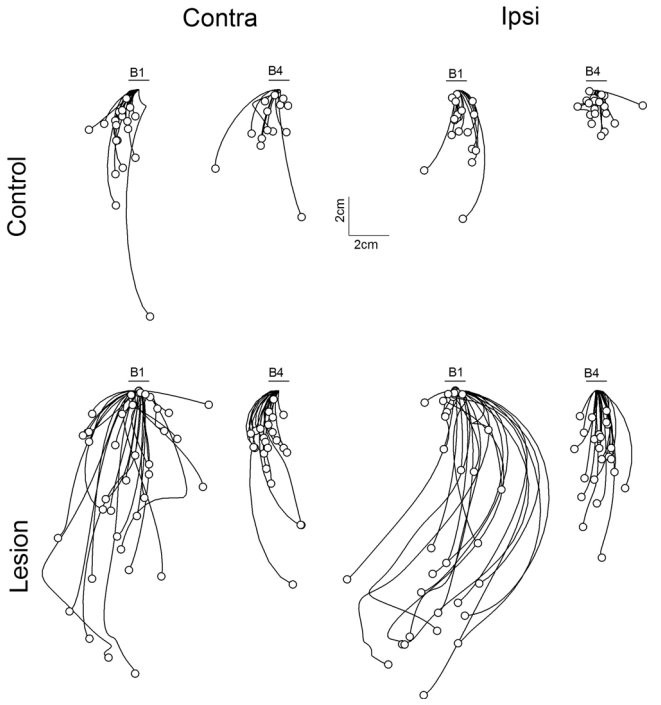

Fig. 11. Representative control (top) and lesion (bottom) withdraw phase trajectories are plotted for left and right hands from a single trial during block 1 and 4. Note: Start location (midpoint of each horizontal line) was standardized to the origin for all trajectories and the end location is indicated by the open circle.

nor the Group x Block interaction, [$F(3,30) = 0.458$, $p = 0.713$, $\eta_p^2 = 0.044$], were significant. The ANOVA (G-G, $\varepsilon = 0.577$) conducted movement scaling for the ipsilateral-to-lesion hand failed to reveal a significant effect of group [$F(1,10) = 4.545$, $p = 0.059$, $\eta_p^2 = 0.312$], block [$F(1.732,17.318) = 0.183$, $p = 0.907$, $\eta_p^2 = 0.018$], and Group x Block interaction [$F(1.732,17.318) = 0.338$, $p = 0.798$, $\eta_p^2 = 0.033$].

4. Discussion

This is the first study to examine the effects of rat forelimb area cortex lesion on movements associated with coordinated use of both hands during a string-pulling task [6]. Rats quickly learn to pull on a string with alternating rhythmic reach, grasp, and withdraw movements of left and right hands in order to obtain a food reward attached to its end. Periodic testing over 70-days indicated that the travel distance of each hand during a trial became shorter with practice, suggesting that optimal string-pulling involves rapid and relatively short forelimb excursions between the chin and body midline, largely directed in a vertical plane, that improves with practice. Forelimb motor cortex lesions disrupted the rhythm and kinematics of string-pulling by both hands in the immediate post-lesion period. After a week of further training, rhythmic movements resumed and the reach-withdraw movements of the lesion group also became reduced in amplitude over subsequent testing sessions. Nevertheless, there were persistent changes in string-pulling movements by animals that had received a lesion. Rats in the lesion group made more grasps with both hands that hooked the string between the digits, their reach and pull distances were longer than those of control rats, and these changes were more pronounced for the ipsilateral-to-lesion vs contralateral-to-lesion hands. Rats in the lesion group also more frequently grasped the string in their mouth than

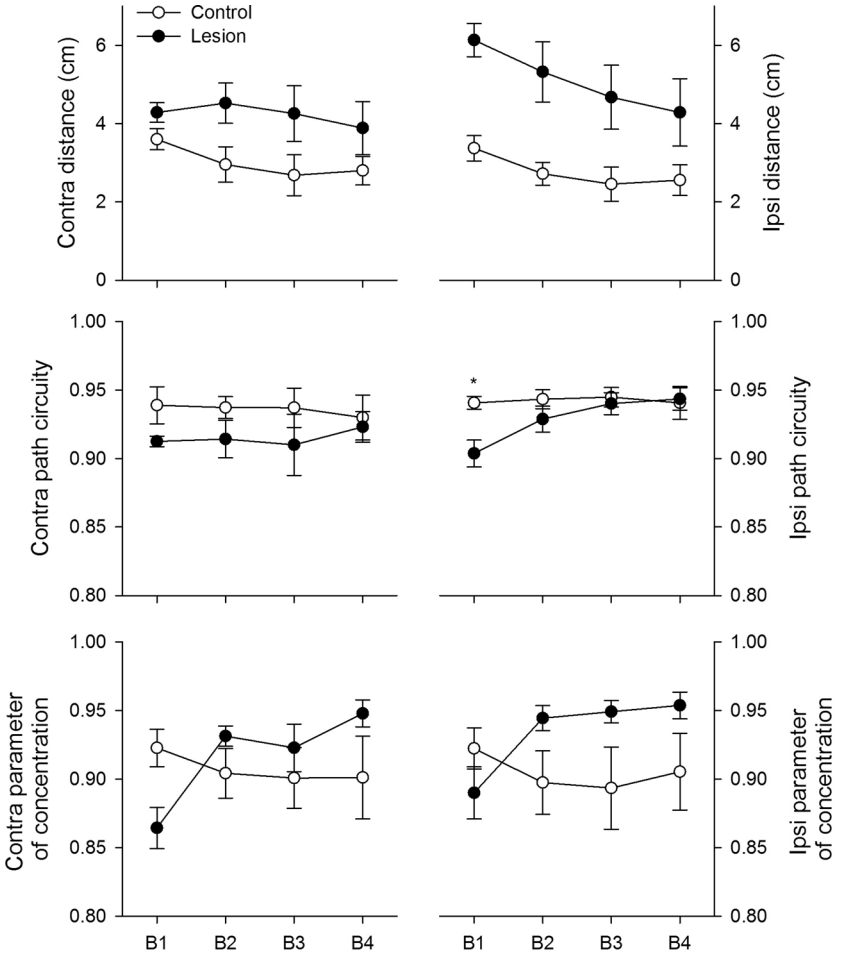

Fig. 12. Average distance traveled for the left (top left) and right (top right) hands during withdraw phases is plotted for both groups across testing blocks. Average path circuity for the left (middle left) and right (middle right) hands during withdraw phases is plotted for both groups across testing blocks (*$p < 0.05$). Average parameter of concentration for the left (bottom left) and right (bottom right) hands during withdraw phases is plotted for both groups across testing blocks.

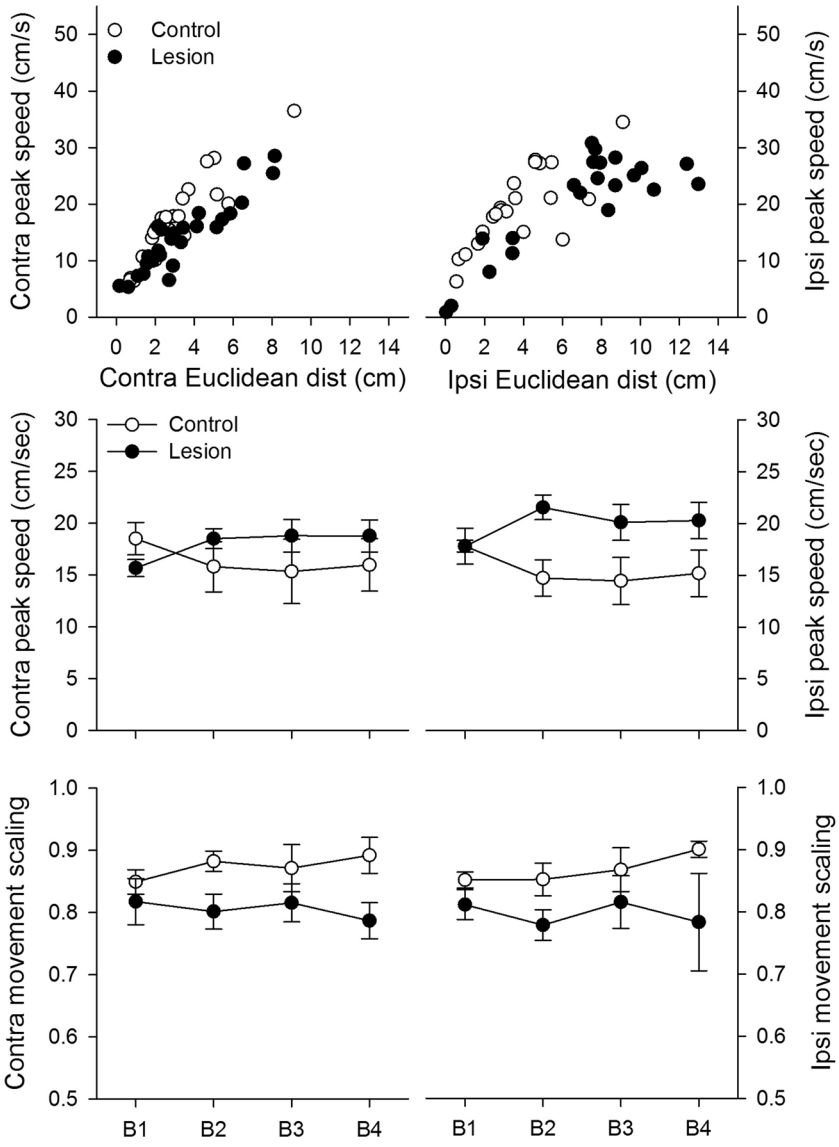

Fig. 13. Peak speeds and Euclidean distances are plotted for all left (top left panel) and right (top right panel) withdraw phases within a single string-pulling trial. Average peak speeds during withdraw phases are plotted for the left (middle left panel) and right (middle right panel) hands across testing blocks. Average movement scaling scores during withdraw phases are plotted for the left (bottom left panel) and right (bottom right panel) hands across testing blocks.

did the control group. Taken together, the results suggest that although the lesion did not chronically affect the rhythmicity of reach-withdraw movements, the limb/hand contralateral to the lesion was impaired. To compensate, the ipsilateral-to-lesion hand did more pulling, with longer reach and withdraw distances, and grasping with the mouth was used to stabilize the string so that the contralateral-to-lesion hand could grasp it.

4.1. Forelimb sensorimotor cortex lesions disrupt string-pulling behavior organization

The string-pulling task differs in a number of ways from spontaneous eating tasks that also involve two-handed manipulation of food items such as eating nuts or pasta [3,25,20,21,43,42,44,45]. For spontaneous eating, both hands move in synchrony to bring food to the mouth and both hands are concurrently involved in holding the food for eating. In spontaneous eating, if one hand is impaired by a central lesion, the unaffected hand can compensate by performing most of the manipulatory movements required to keep food in the mouth. The string-pulling task involves the coordinated movement of both hands in which at any moment the task of each hand is different, one hand reaches as the other withdraws. For string-pulling, if one hand fails to grasp on a reach, or fails to withdraw after grasping, the string can be lost when the other hand releases it after a withdraw. Nevertheless, following a forelimb sensorimotor cortex lesion, the rats perform the task surprisingly well, although, as the following will explain, they do so using a variety of compensatory adjustments of both hands and of the mouth [1].

The performance of string-pulling for food was observed over a relatively long duration of 70 days. Although the rats learned the task quickly, they continued to refine their reach-withdraw movements over the testing period. Initially reaches and withdraws on the string were relatively long, with the reach often extending above the level of the mouth to grasp the string and the withdraw extending below the level of body midline before it was released. Over the course of testing, the reach-withdraw movements became shorter, with both phases occurring mainly between the level of the mouth and the body midline. Longer reaches and withdraws were associated with higher peak speeds and accordingly, asymptote performance featured slower and more deliberate reach-withdraw movements. A characteristic feature of string-pulling was its rhythmicity, with left and right hands alternating with similar reach and withdraw distances and speeds and with the direction of movement concentrated in the vertical plane. String grasps occurred mainly with a medially directed hand movement in the horizontal plane in which the digits were fully opened and extended in preshaping and then closed to grasp the string in a whole hand grasp.

Although, testing took place over a relatively long duration, testing was done weekly, and thus the general findings of the present experiment could be confirmed by allowing animals more practice with daily training.

Devascularization was observed to damage the RFA and the CFA portions of the sensorimotor cortex. Although the neither the RFA nor the CFA were completely destroyed, afferent and efferent connections between the RFA and the CFA were likely lost. The resulting damage produced both acute and chronic changes in string-pulling behavior. In the acute period, extending over the first post-lesion week, latency to initiate and perform string-pulling increased and the rhythmicity of the movements was fragmented. Nevertheless, both hands continued to participate in string-pulling. By the second block of testing, the rhythmicity of string-pulling was largely restored such that string-pulling proceeded with alternating movements of the ipsilateral-to-lesion and contralateral-to-lesion hands. For murids as for primates, the corticospinal tracts have both crossed and uncrossed projections with the uncrossed projections mediating more proximal movements [33]. Possibly, the relatively rapid recovery in rhythmicity of string-pulling behavior was in part mediated by uncrossed projections from the unaffected hemisphere to the contralateral-to-lesion hand. Additionally, because unilateral stimulation of murid motor cortex can produce alternating movements in both limbs [19], it may be that the intact hemisphere can support the rhythmical movements required of string-pulling. Further, the spared RFA and CFA may have been sufficient to mediate improvements in performance observed over time. Future work with more complete lesions restricted to either area may produce a double dissociation in string pulling behavior.

Although the rats that had received sensorimotor cortex lesions displayed progressively reduced amplitude of reach-withdraw excursions over the testing period, as did rats in the control group, their excursions were consistently longer than were those of the control group. In addition, the amplitude of the reach and withdraw movements of the ipsilateral-to-lesion hand were longer than were those of the contralateral-to-lesion hand. This finding suggests that following sensorimotor cortex injury, rats rely more on the ipsilateral-to-lesion hand than the contralateral-to-lesion hand to advance the string. In addition, the use of a hooking motion to grasp the string between the digits, rather than across the palm of the hand, were made more frequently in the ipsilateral-to-lesion hand vs than the contralateral-to-lesion hand. The increased amplitude of reach, in which the string was grasped by a vertically directed rather than horizontally directed movement by the ipsilateral-to-lesion hand may responsible for the increased incident of hooking the string between the fingers.

The rats with forelimb sensorimotor cortex lesions made more misses when attempting to grasp the string with the contralateral-to-lesion hand than did the control group. They also made more frequent use of grasps of the string with the mouth. It is possible that the mouth grasp is a strategy used by the lesion rats to stabilize the string, so that it can be more easily grasped by the contralateral-to-lesion hand. Indeed, a typical grasp strategy of the rats when using the contralateral-to-lesion hand involved grasping the string in the mouth and then reaching to grasp the string just above the mouth. For the control rats, grasps were made using one hand as the other was pulling on the string and so generally, both hands and the string were in motion during grasps. Furthermore, because string pulls were made in the vertical plane, the string was moving through the vibrissae sensory field, thus allowing the rats to track the strings (especially with vibrissae 6–7 in rows C,D,E) motion with snout movement. An impairment in use of the contralateral-to-lesion hand was possible due to difficulty in directing the hand in relation to vibrissae cues that localized the string.

4.2. Representation of manipulatory scale movement

Previous work has demonstrated that the scale of movement fundamentally changes the nature of the representation that is encoded [35]. Several lines of evidence suggest that common representational system may guide performance across ambulatory and manipulatory scales of movement. First, behavioral studies have demonstrated that rats use a vector or polar coordinate system to encode the location of a goal on land and water mazes [8,39,17]. Similar effects have been observed in humans performing in a manipulatory scale analogue of the Morris water task [31]. Next, electrophysiological studies have discovered neural signals that are tuned to direction [41] and distance [27] aspects of ambulatory scale movement. Similar directional coding of movement has been observed in manipulatory scale movement [14]. Finally, evidence suggests that manipulatory scale neural systems evolved from brain structures that mediate ambulatory scale movement [15,22,26]. Therefore it is possible that a directional vector representational system was used to guide movement during string puling behavior.

Several lines of evidence are consistent with lesion producing an impaired ability to estimate direction and distance manipulatory scale movement. First, the lesion was observed to produce an acute reduction in the heading consistency of reach and withdraw trajectories on the first block of testing. This bilateral disruption was observed during both reach and withdraw phases. Damage to cortical areas mediating direction estimation may have resulted in less accurate neural systems guiding trajectory direction estimation. Next, the lesion group exhibited a significant increase heading consistency across subsequent testing blocks that exceeded performance observed in the control group. This effect was also observed bilaterally and during both movement phases. These less accurate neural systems support sufficient flexibility to support motor leaning; however, the end result is highly stereotyped pattern of directed movements. Finally, a reduction in movement scaling was observed during withdraw phases, with significant reductions restricted to the ipsilateral-to-lesion hand. Weaker movement scaling was observed to persist throughout testing, consistent with impaired distance estimation. These observations are consistent with the lesion damaged cortical regions that contribute to estimating direction and distance of hand position within manipulatory space. Loss of these representational characteristics may have prompted the lesion rats' strategy of using the mouth to stabilize and hold the string to assist string-pulling.

4.3. String-pulling as a potential behavioral therapy

There are two main strategies used to assist in the rehabilitation of hand movements after lesion, including constraint-induced therapy [11,40], in which the less affected hand is constrained to facilitate use of the more affected hand, and bilateral hand therapy [12], in which the therapeutic task encourages use of both hands. Previous work has shown that intensive bimanual training improves hand use in children with unilateral cerebral palsy [9] and largest improvements in hand use were related to motor cortex plasticity [13]. Furthermore, synaptic changes are observed bilaterally in layer V motor cortex after string pulling experience [29].

The string-pulling task is an ideal way of administering bilateral hand therapy. In the string-pulling task, success depends on the contribution of both hands but the degree to which each can participate is left open. The conjoint use of both limbs allows the movement of the less affected limb to contribute to the movement of the more affected limb and it also allows the more affected limb to increase its participation as rehabilitation/recovery proceeds. The task is easy to administer and tasks demands can be readily adjusted with respect to speed, complexity, or force. Indeed, the inherent procedure of the string-pulling task as used here over a prolonged post-lesion period may have underestimated the effects of the forelimb motor lesion on hand use because the task enforced rehabilitation throughout testing.

4.4. Conclusion

The current study demonstrated that unilateral sensorimotor cortex lesions disrupt the organization of string-pulling behavior. The changes in movement organization reflect a loss of the contralateral-to-lesion fine motor control that is compensated for by modification of ipsilateral-to-lesion motor function and increased mouth grasping. These changes in performance remained stable across weekly testing sessions. Future work should be directed at evaluating the sensory control of string pulling (e.g., the role of the vibrissae in tracking the string), examining the role of trunk movement in stabilizing the body so that individuated movements of the forelimbs can occur, examining the organization of string-pulling in other animals including humans, and further investigating the use of the task for rehabilitation in both rodent models of human diseases and in humans with motor system injury.

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