Complete and Partial Lesions of the Pyramidal Tract in the Rat Affect Qualitative Measures of Skilled Movements: Impairment in Fixations as a Model for Clumsy Behavior

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ABSTRACT

Little is known about prenatal and perinatal brain injury resulting in subsequent clumsy behavior in children. One candidate motor system is the pyramidal tract. The tract traverses the entire central nervous system and, through direct and indirect connections to the brainstem and spinal cord sensory and motor nuclei, is involved in the learning and execution of skilled movements. Here, rats, either naïve or pretrained on a number of motor tasks, were assessed for acute and chronic impairments following complete or incomplete pyramidal tract lesions. Postsurgery rats with complete lesions were impaired on the qualitative measures of limb aiming, supination, and posture. Impaired movements require fixations, complementary movements in different body segments. The impairment in fixations was manifest acutely and underwent no improvement with subsequent training/testing. The finding that complete and partial pyramidal tract lesions produce chronic impairment in fixations provides insight for understanding clumsy behavior in humans and its potential remediation via specific training in making fixations.

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KEYWORDS

clumsy behavior and pyramidal tract, fixations and clumsy behavior, fixations and pyramidal tract, partial pyramidal tract lesion, pyramidal tract and placing, skilled movement, skilled reaching

INTRODUCTION

Although the pyramidal tract was once thought to be the substrate of all voluntary movement, it is now apparent that many movements survive pyramidal tract section (Ruch et al., 1965). In all species studied, the use of limbs for skilled movements appear more affected than the use of limbs for locomotion (Lawrence & Kuypers, 1968; Metz et al., 1998; Muir & Whishaw, 1999). Studies on the of forelimbs in tasks requiring reaching for food or manipulating levers indicate that relatively independent use of the movements of the digits, rotatatory movements of the limb, and response speed are most affected (Alstermark et al., 1989; Lawrence & Kuypers, 1968; Whishaw et al., 1993). Many studies of pyramidal tract function have included animals with partial lesions to the pyramidal tract. In general, partial lesions reportedly result in substantial sparing of movement (Hepp-Reymone & Wiesendanger, 1971; Laursen, 1971; Lawrence & Kuypers, 1968; Lawrence & Hopkins, 1976). Bucy and coworkers

(1964; 1966) report the most dramatic example of functional sparing. Their human subject had only 17 percent of the pyramidal tract on one side spared, and he recovered substantial use of the affected limbs, hand, and digits.

The rat is widely used for studies of recovery and restitution of function, and the pyramidal tract is extensively used a model system for such studies (Goodman et al., 1966; Gribnau et al., 1986; Hyland & Jordan, 1997; Joosten et al., 1992; Kalil K, 1975; Kartje-Tillotson & Castro, 1980; McKenna & Whishaw, 1999; McKenna et al., 2000; Metz & Whishaw, 2002; Miller, 1987; Thallmair M, 1998; Vahlsing & Feringa, 1980; Z'Graggen et al., 1988). After complete lesions of one pyramidal tract above the pyramidal decussation, rats display a number of abnormalities in the use of the forelimb contralateral to the lesion.

1. When suspended by the tail, rats adduct rather than extend the contralateral forelimb (Barron, 1938; Whishaw & Metz, 2002). In tests of placing, rats display impairments in using the contralateral forelimb (Whishaw & Metz, 2002). In tests of placing, rats display impairments in using the contralateral forelimb (Whishaw & Metz, 2002).
2. When give a choice of using the forelimbs for reaching for food, they show a preference for the ipsilateral forelimb (Kartje-Tillotson & Castro, 1980; Whishaw & Metz, 2002).
3. When forced to use the contralateral forelimb rats display reduced success in obtaining food (Whishaw et al., 1998; Whishaw & Metz, 2002; Whishaw et al., 1993).
4. Even when rats are successful in obtaining food, rotatory movements of the limb, including pronation and supination, are abnormal (Whishaw & Metz, 2002; Whishaw et al., 1993).

The extent to which these various symptoms can be obtained in animals with partial lesions to the pyramidal tract is not known. Such information would be useful for a number of reasons. It would aid determining the size of a lesion required for experimental investigations and would also be relevant to understanding the extent of recovery that might be expected in studies directed toward sparing or restoring the functional integrity of portions of the pyramidal tract. Additionally, chronic impairments in movements could potentially be manifest as clumsy behavior in humans, thus presenting the pyramidal tract as a candidate neural substrate for clumsy behavior.

In the present study, groups of rats received no lesion, a partial pyramidal tract lesion, or a relatively complete pyramidal tract lesion. Their performance on tests sensitive to complete lesions of the pyramidal tract were compared in both naÔve and trained rats and in acute and chronic phases following the lesion.

EXPERIMENTAL

Subjects

Subjects were Long Evans adult female rats (n†=†64) weighing 180 to 200 g each when the study began. The rats were housed in pairs in hanging Plexiglas cages in an animal colony lighted on a 12:12 light-dark cycle with lights off at 20:00 h. Testing was done during the light portion of the cycle. The U. of I. Animal Care Committee approved the experiments according to guidelines established by the Canadian Council on Animal Care.

Surgery and lesion placement

For surgery, the rats were anesthetized with isofluorane anesthesia. Thirty-nine animals were given unilateral pyramidal tract lesions and twenty-one rats served as the control group. A ventral midline incision was made, the sterno-hyoid and sterno-thyroid muscles on one side were split longitudinally and retracted, and the trachea and esophagus were slightly displaced. With the use of an operating microscope, a blunt deep dissection revealed the outer surface of the occipital bone and the ventrocaudal part of the bone was partially removed with a dental burr. The medullary pyramid (namely, the corticospinal tract) was thus exposed above the decussation and the pyramid was incised with a sharp No. 11 scalpel blade and dissecting tweezers. The esophagus, trachea, and muscles were repositioned and the skin sutured (Whishaw et al., 1993).

Food deprivation

Before training on the reaching tasks began, the rats were food deprived. From then on, after each training session, the rats were provided with a measured amount of food each day to maintain body weight at about 90 percent.

Video recording

Video records were made with a Sony Video 8 CCD VII portable camera having a shutter speed of 1000th of a second. A two-arm Nikon Inc. MII cold light source provided illumination for high shutter speed filming. Frame-by-frame analysis at 30 to 60 frames per second was provided by a Sony Video 8 recorder or through a computer-based frame grabber (Whishaw & Pellis, 1990).

Limb posture test

Rats were gently lifted by the tail from a horizontal surface, and the posture of each forelimb in the suspended animal was rated (Barron, 1938; Whishaw & Metz, 2002; Whishaw et al., 1981). If a forelimb was extended ventrally and laterally, as if the rat were attempting to obtain purchase with a substrate, then a score of '0' was given. If the forelimb was adducted upward toward the ventral surface of the animal's body by at least 45 degrees, then a score of '1' was given.

Placing test

A cylinder (30 cm high, 16 cm dia) was made of 3 mm thick Plexiglas. The cylinder was mounted on a glass table beneath which was positioned an inclined mirror. For a test, a rat was placed into the cylinder and left to explore for 5 min, during which its behavior was filmed. Contacts of the forepaws with the wall of the cylinder were counted upon reply of the videotape (Johnson et al., 1999). The results were scored using the following formula:

Percent contacts = right paw contacts/(right paw contacts + left paw contacts) x 100.

Reaching boxes

Two types of test boxes were used (Whishaw, 2000; Whishaw & Miklyaeva, 1996). Food tray boxes (10 wide x 18 long x 10 cm high) were constructed of Plexiglas with a face consisting of 2-mm bars spaced 9-mm apart, edge to edge. A 4-cm-wide and 5-cm-deep tray, containing granules of food (20 to 40 mg chick feed) was mounted in front of each box and extended for the length of the box. To obtain food, the rat had only to reach through the bars to grasp and retract it. The floor was made of grids so that if a rat dropped the food, it fell through the grids and was lost (Whishaw et al., 1986).

Single-pellet boxes were made of clear Plexiglas so that the rats could be filmed from any perspective (Whishaw & Pellis, 1990). A box was 25 cm wide x 35 cm long x 30 cm high. Five cm from the side of each front wall was a 1-cm-wide slit that extended from the floor to a height of 15 cm. On the outside of the wall, in front of the slit mounted 3 cm above the floor was a 2-cm-wide by 4-cm-long shelf. Food pellets (90 mg Rodent Chow food pellets, Bioserve Inc., Frenchtown, New Jersey, USA) were placed in one of two small indentations of the floor of the shelf. The indentations were 2 cm away from the inside wall of the box and were centered on the edges of the slit through which the rats reached. For each rat, food was placed in the indentation contralateral to the limb with which the rat reached. Training was administered in such a way that when a rat made a successful reach, a short pause preceded the presentation of the next food pellet, during which another food pellet was sometimes dropped into the back of the box. This was done to ensure that a rat left the food aperture after each reach and repositioned itself at the food aperture for the next food pellet.

Bracelets for limb restraint

To force a rat to use the desired limb for reaching, we placed a bracelet on the opposite limb. A bracelet attached to a rat's arm prevents the rat from inserting that arm through the aperture to grasp food but did not otherwise impede limb movement lost (Whishaw et al., 1986). A strip of elastic plaster (Elastoplast, Smith and Nephew, Lachine, Quebec, Canada) 2.5-cm wide and about 6-cm long was used with a rectangle (1.5-cm by 1.25-cm) cut out of one its ends. The plaster was folded sideways so that the sticky sides faced each other, laving only the remaining uncut section on one end with an exposed adhesive surface. The elastic was wrapped around a rat's forearm and fixed with the exposed plaster. The thickness of the bracelet around the forearm could be controlled by varying the length of the plaster tape, thus varying the number of wraps around the forearm. The bracelets could be slipped off after use and did not denude the rat's forearm of hair. Once the rats became habituated to the bracelets the animals usually ignored them. Usually, after habituation, the rats learned to use their nonpreferred limb even when the bracelets were not in place.

Scoring reaching *success*

For a reaching test, rats reached for 10 min in the tray task and reached for 20 food pellets in single pellet task. Reaching performance was scored by counting misses and successful reaches for each limb. If a rat made a reaching movement in which a paw was inserted through the bars/aperture of the cage, then the movement was scored as a 'reach'. If a rat obtained a piece of food and then consumed it, then the reach was scored as a 'hit'. For each test, a hit percent score was obtained using the following formula:

Hit percent = number of hits/number of reaches x 100

Movement analysis

Movements were analyzed using a rating scale derived from Eshkol-Wachman Movement Notation (Eshkol & Wachman, 1958). In brief, EWMN is designed to express relations and changes of relation between the parts of the body. The body is treated as a system of articulate axes (namely, body and limb segments). A limb is any part of the body that either lies between two joints or has a joint and a free extremity. These are imagined as straight lines (axes) of a constant length that move with one end fixed to the center of a sphere. An important feature of EWMN is that the same movements can be notated in several polar coordinate systems. The coordinate of each system are determined with reference to the environment, to the animal's body midline axis, and to the next proximal or distal limb or body segment. By transforming the description of the same behavior from one coordinate system to the next, invariance in that behavior can emerge in some coordinate system but not in others. Thus,

TABLE 1

Behavior	Normal	Impaired
Digits in the midline	0	1
Digits flexed	0	1
Elbow in	0	1
Advance	0	1
Digits extend	0	1
Arpeggio	0	1
Grasp	0	1
Supination I	0	1
Supination II	0	1
Release	0	1
Total		10

the behavior can be invariant in relation to some or all of the following: the animal's longitudinal axis, gravity, or bodywise in relation to the next proximal or distal segment. On the basis of descriptions obtained from EWMN rating scales of movements were derived. Five reaches for each limb by each rat were rated for qualitative features of the movement (Whishaw et al., 1993). A movement scale rating is shown in Table 1, and 10 component movements of reach were rated.

1. Digits in the midline: Using mainly the upper arm, the reaching limb is lifted from the floor so that the tips of the digits are aligned with the midline of the body.
2. Digits flexed: As the limb is lifted, the digits are flexed, and the paw is supinated and the wrists partially flexed.
3. Elbow in: Using an upper arm movement, the elbow is adducted to the midline while the tips of the digits retain their alignment with the midline of the body.
4. Advance: The limb is advanced directly through the slot toward the food target.
5. Digits extend: During the advance, the digits extend so that the digit tips are pointing toward the target.
6. Arpeggio: When the paw is over the target, the paw pronates from digit 5 (the outer digit) through to digit 2, and at the same time the digits open.
7. Grasp: The digits close and flex over the food, and with the paw remaining in place and the wrist slightly extended to lift the food.
8. Supination I: As the paw is withdrawn, the paw supinates by almost 90 degrees.
9. Supination II: Once the paw is withdrawn from the slot to the mouth, the paw further supinates by about 45 degrees to place the food in the mouth.
10. Release: The mouth contacts the paw and the paw opens to release the food.

Each movement was rated on a 3-point scale. If the movement was performed normally, then a score of '0' was given. If the movement was abnormal, then a score of '1' was given. In cases of some ambiguity concerning the occurrence of a movement, a score of '0.5' was given.

Reaching posture

On each reach, the posture used by the rat was rated on a 2-point scale (Whishaw & Metz, 2002; Whishaw et al., 1993). If a rat supported itself on the contralateral-to-reaching paw forelimb and its diagonal hind limb as the reach was initiated, then a score of '0' was given. If a rat failed to use this supporting posture, then a score of ì1î was given. The evaluation of reach posture included scoring the rat's approach to the slot: whether a rat positioned its body on a diagonal ipsiversive, diagonal contraversive, or orientated straight on to the slot was recorded.

Histology

At the conclusion of the experiment, the rats were deeply anesthetized with sodium pentobarbital and perfused through the heart with a 0.9% NaCl-PFA solution. The brains were removed and the ventral surface of the brain containing the lesion was photographed. The brains were cut at 40 µ on a mictrotome and the sections stained with Schmeud (1990) gold chloride myelin stain.

Time line

Animals were tested according to one of two experiment protocols. In the first experiment, the rats (n=50) were allowed 2 wk for recovery following pyramidotomy of the right hemisphere. The rats received a test for limb posture 1 d following surgery and again at the completion of all other tests. Two wk following surgery, the rats received a placing test. On the following day, the rats were food deprived and placed into the food tray reaching boxes for 1 h each day for 14 d. On day 15, reaching success was recorded. On the following day, each rat received a bracelet on its preferred paw before training and was trained for a further 14 d in the tray task. On the 15th day, the rats were tested. On the next day, the rats began training in the single-pellet task, which continued for 15 d for one forepaw and then for another 15 d for the second forepaw.

In the second experiment, the rats (n=10) were trained to perform the single-pellet reaching task until a stable success level was achieved. The animals then received lesions contralateral to the preferred paw, and testing was resumed the following day. The number of pellets retrieved was scored for 14 d, and successes were video recorded one day before, one day following, and 14 days following surgery.

Statistical analysis

The results were assessed using analysis of variance (ANOVA) follow-up Newman-Keuls tests and with Mann-Whitney U tests.

RESULTS

Histology

At the completion of the experiments, the photographs were examined by a histologist who was naïve to the performance of the animals. The animals with lesions restricted to the pyramidal tract were separated into a group composed of animals having partial lesions and into a group composed of animals having complete lesions (Fig. 1).

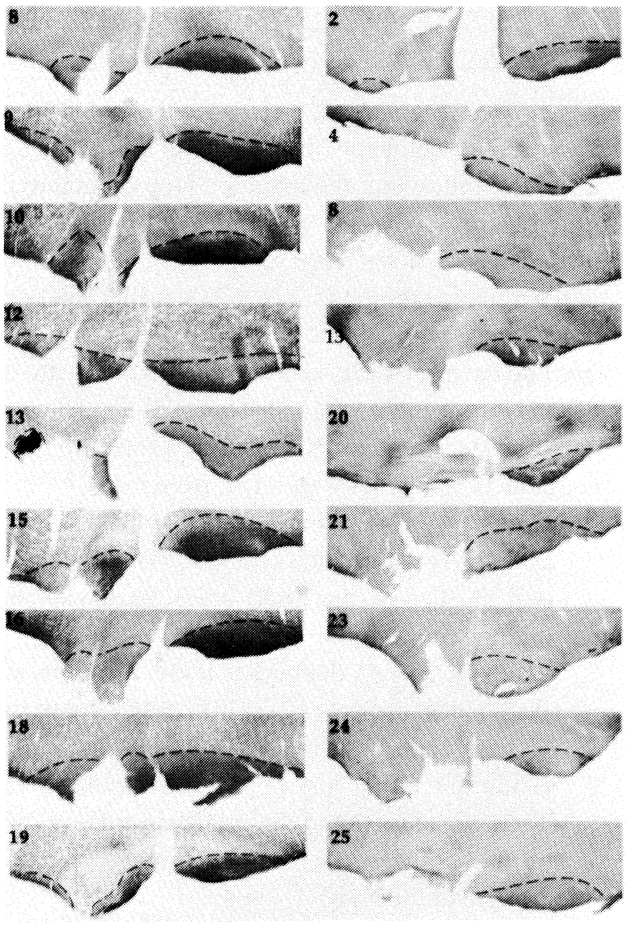

Fig. 1: Representative histological results from partial lesion (left) and complete lesion (right) rats. Photomicrographs of ventral view of medulla show the pyramidal tracts. Dotted lines indicate the location of the pyramidal tract. (Schmeud (1990) gold chloride myelin stain. Coronal sections).

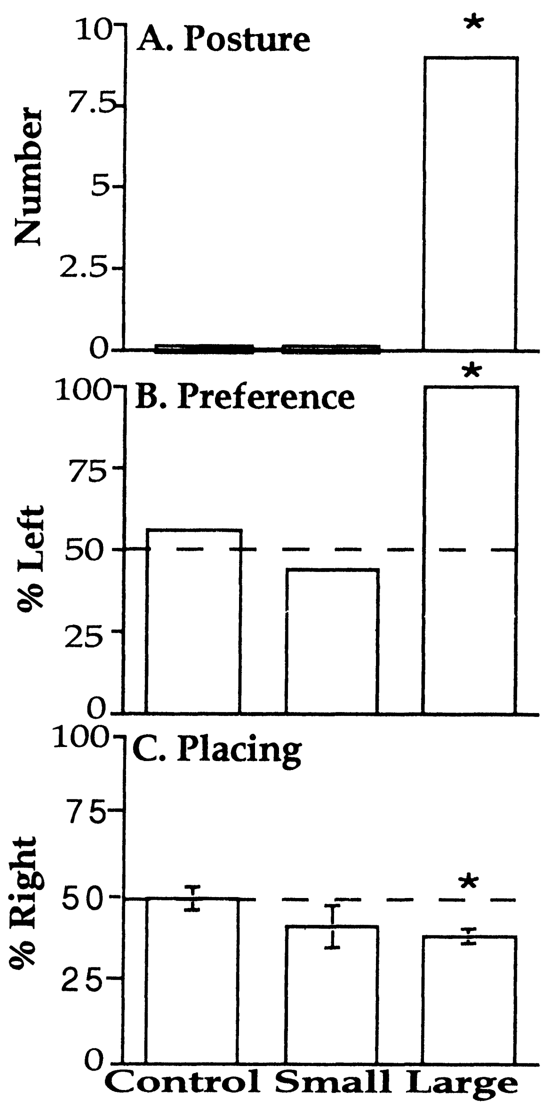

Fig. 2: Limb performance (mean and SE) of control and pyramidal tract lesion (lesion) rats on three tests of limb use (right paw = paw contralateral to the lesion). A. *Posture.* Rat was held by the tail, head down, and the number displaying forelimb adduction with the contralateral forelimb was counted. B. *Reach.* The number of rats displaying a preference for a particular forepaw when initially trained to reach in the tray-reaching task. C. *Placing* in the cylinder test. Contacts with the wall by each forepaw were counted. Note that rats with complete pyramidal tract lesions displayed significantly (**p<0.05) more postural abnormalities in the paw contra-lateral to the lesion, preferred the ipsilateral paw for reaching, and made significantly fewer contacts with the cylinder with paw contralateral to the lesion.

Limb posture

A significant Group effect in limb flexion was observed when the rats were suspended by the tail (Mann-Whitney U test, $U = 0$, $p > 0.05$, Fig. 2A). All nine rats with large pyramidal tract lesions adducted the paw contralateral to the pyramidal tract section (right paw). No abnormalities were observed in the left paws of this group. No impairment was observed in either paw of the rats with small lesions or no lesions.

Placing test

An ANOVA on the relative number of contacts with the ipsilateral limb against the horizontal wall of the cylinder during raring revealed no group effect ($F(2,31) = 2.05$, $p = 0.14$). Because the variance in the small lesion group was high, separate F-tests were used to compare the control group with the lesion group, which indicated that the control and large lesion groups were different, ($F(1,23) = 5.2$, $p = 0.03$), but the control and the small lesion groups were not.

Limb preference for reaching

When first trained on the tray reaching test, nine control rats reached with the left paw and seven reached with the right paw. Among the small lesion group, four reached with the left paw and five reached with the right paw. All rats with large pyramidal tract lesions reached with paw ipsilateral to the lesion (left paw), a result that differed significantly from chance ($t = 0.5$, Fig. 2B).

Tray task reaching

All rats were allowed to reach for 14 d, upon which they were given a 10 min test for reaching success. Then, using bracelets, the rats were forced to use their non-preferred paw while being trained

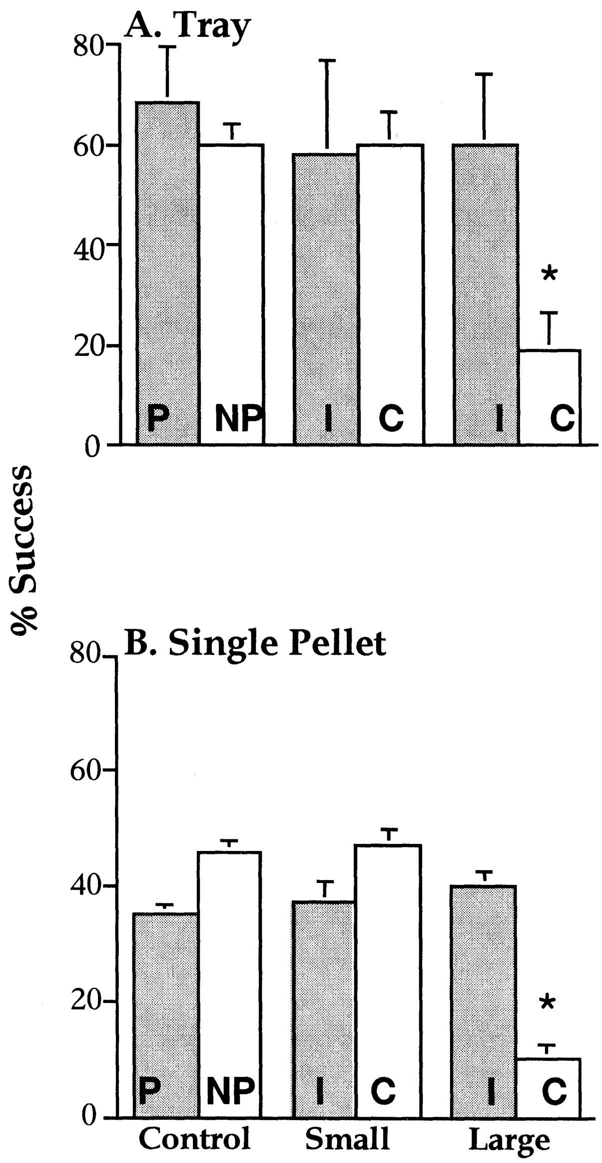

Fig. 3: Reaching success (mean and SE of percentage scores) displayed by control and pyramidal tract lesion rats when reaching in the tray task and the single pellet task with the preferred paw (NP, the contralateral forepaw that was used following forced training) or the paw ipsilateral (I) or the paw contralateral to the lesion (C). Note: No differences in success were displayed by control or partial lesion rats when using either paw. Performance using the ipsilateral-to-lesion paw by the complete lesion pyramidal tract group did not differ from control performance. Performance using the paw contra-lateral (C)-to-lesion by the contralateral group was significantly (*$p < 0.05$) impaired in both tasks.

for a further 14 d. The animals were then given a second 10-min test for reaching success. The results of both tests are summarized in Fig. 3A. An ANOVA on the hit percent scores indicated a significant effect of Group ($F(2,31) = 11.9$, $p = 0.002$), of Paw $F(1,31) = 18.4$, $p = 0.002$), and a significant Group by Paw interaction, ($F(2,31) = 11.6$, $p = 0.002$). Follow-up Newman-Keuls tests indicated no differences in performance between the control group's preferred and non-preferred paws nor between the small pyramidal tract lesion group's ipsilateral-to-lesion and contralateral-to-lesion paws. There was a significant difference between the large pyramidal tract lesion group's ipsilateral-to-lesion and contralateral-to-lesion paws. The contralateral paw was impaired ($p < 0.05$). There was no difference in performance between the pyramidal tract group's ipsilateral-to-lesion and either paw of the control group or the small lesion group.

Single pellet reaching task

All rats were allowed to reach for 14 d and the hit percent was recorded each day. Then, using bracelets, the rats were forced to use their non-preferred paw while being trained for a further 14 d. Again, hit percent in obtaining 20 single pellets was recorded each day. An ANOVA was performed on the average hit percent scores of the last 4 days of training. The results summarized in Fig. 3B indicated a significant effect of Group ($F(2,32) = 7.7$, $p = 0.009$) and no effect of Limb, but there was a significant Group by Limb interaction, $F(2,32) = 17.6$, $p = 0.001$. Follow-up Newman-Keuls tests indicated no difference in performance between the control group's preferred and non-preferred paws or between the small lesion group's ipsilateral and contralateral paw. There was a significant difference between the large lesion pyramidal tract group's ipsilateral-to-lesion and contralateral-to-lesion paw. The contralateral paw was impaired ($p < 0.05$). There was no difference in performance between the pyramidal tract group's ipsilateral-to-lesion and either paw of the control group or the small lesion group.

Single pellet reaching movement analysis

For the qualitative analysis of reaching, the videotape of the reaches was replayed frame-by-frame, and a reach comprising 10 movements was rated on a 0 to 1 point scale. One videotape containing data on one control and one large pyramidal tract lesion rat was corrupt so both rats were excluded from the analysis. An ANOVA of performance indicated significant main effects of Group ($F(2,28) = 12.5$, $p = 0.001$), of Paw $F(1,28) = 18.2$, $p = 0.001$), and a significant Group by Paw inter-action, ($F(2,28) = 8.1$, $p = 0.001$). The large lesion group obtained higher ratings than did the small lesion group.

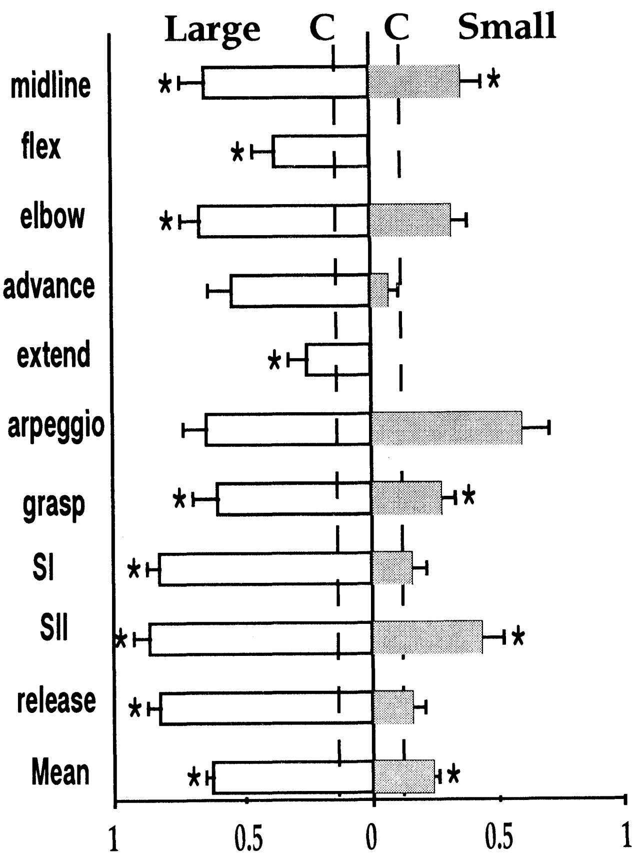

Fig. 4: Qualitative ratings (mean and SE) on movement components of reaching in control (C) and large and small pyramidal tract groups. Note that both the large and small lesion groups displayed impairments but the impairments were smaller and occurred on fewer movements in the small pyramidal tract group. Each movement was rated on a 2-point scale: 0 = normal; 1 = impaired. *$p < 0.05$.

An analysis of which elements of the reach were affected revealed a significant effect of elements, ($F(9,243) = 18.9$, $p = 0.001$) and a significant Group by Element interaction, ($F(18.243) = 5.3$, $p = 0.001$). Figure 4 provides a summary of element scores, showing that whereas the large lesion group differed from the control group on most element scores, the small lesion group also differed from the control group in a number of element scores, including bringing the paw to the midline, grasping food, and supinating the paw to present food to the mouth.

Qualitative description of movements

An analysis of posture revealed a significant Group effect ($F(2.28) = 11.5$, $p = 0.001$), and follow-up tests indicated that the control group obtained a significantly higher score that did either lesion group, which did not differ. Figure 5 illustrates a typical postural difference between a large lesion rat (yellow) and a control rat (blue) at four different times during the reach. The green area shows areas of overlap. The figure was made by superimposing photos of the rats as they performed different components of the reach From this figure, it is clear that the movements used used by the two rats are different. Notably, the rat with the pyramidal tract lesion (a) uses a diagonal approach to the slot, angling in from the right, (b) supports its weight mainly on its good (left) hind limb, and (c) rotates its head ipsiversive to its bad

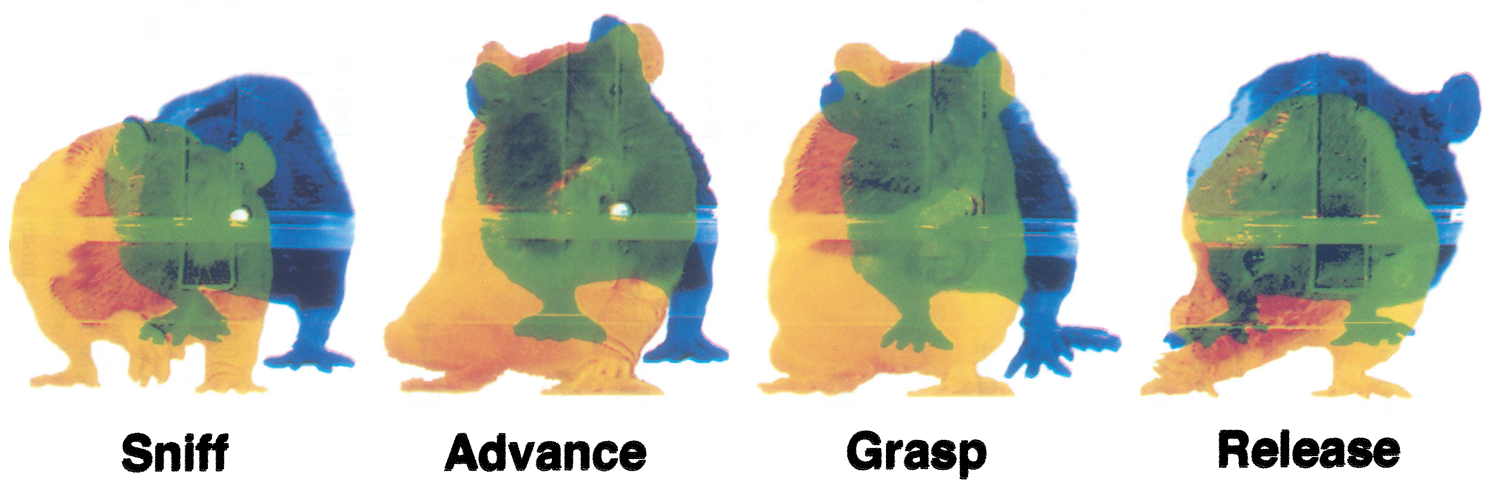

Fig. 5: Posture of a control rat (blue) compared with the posture of a large lesion pyramidal tract rat (yellow) during four stages of a reach. Areas of green area represent areas of overlap. Note the differences in approach, postural support, body rotation, and head rotation during different phases of the reach.

paw to retrieve the food pellet from the paw. Both the small and large lesion groups displayed a significant tendency to use a diagonal approach to the slot, Group (F(2,28) = 16.8, p = 0.001), with both lesion groups making use of this approach more than did the control group.

Whereas the small lesion rats used a diagonal approach to the slot and tended to support their weight mainly on the good hind limb, their most characteristic abnormality was their aim. Figure 6A illustrates the aim of a control rat in which the digit tips and the elbow are aligned to the midline of the body. Figure 6B illustrates that the rat with the small pyramidal tract lesion has the digits lateral to the body midline with the elbow in. Thus, the forelimb is not pointing through the slot, as does the forelimb of the control rat.

Performance of rats with small lesions

To evaluate whether the recovery/impairment displayed by the rats with small lesions was due to compensation derived from the practice received following the lesion, additional rats were trained on the single pellet reaching task, received lesions, and then were tested for 1 d following the lesion beginning on the day following surgery. There were no differences between the groups (F(1,7) = 2.13, p = 0.18), in success in reaching for single food pellets, nor was there any Group by Day interaction (F(1.13) = 0.7, p = 0.17). Thus, the lesion did not affect reaching success. A comparison of the effect of the lesion on the qualitative rating of the 10 movement components on the day before surgery. the day following surgery, and after 14 d gave a significant effect of Group (F(1.21) = 8.7, p = 0.07), and a significant interaction of Group by Test Day (F(2.21) = 4.8, p = 0.18). The rats with small lesions displayed significant impairments in movement on Day 1 and Day 14, but their scores did not differ.

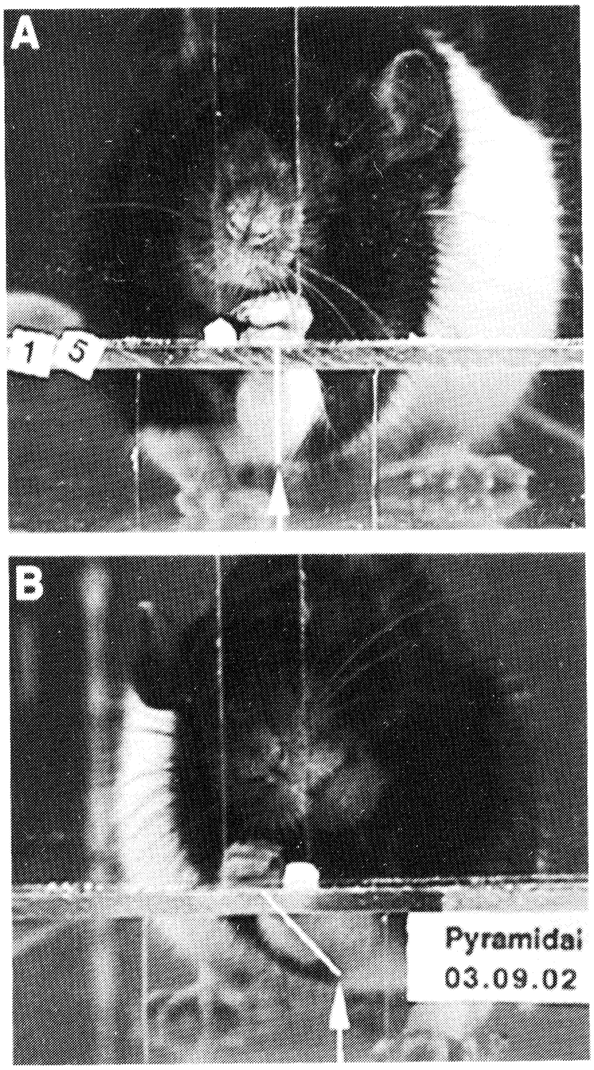

Fig. 6: Example of aiming in a control (A) and a partial pyramidal tract lesions animal (B). For the control animal, the digits and the elbow are aligned with the midline of the body. For the pyramidal tract animal, the elbow is adducted too far medially, and the digits are concurrently adducted away from the body midline. The line and arrow indicate the alignment of the forearm.

DISCUSSION

In the present study, we compared the effect of partial lesions of the pyramidal tract with that of complete lesions of the pyramidal tract in the rat on a number of tests requiring skilled movements. One goal was to determine whether and how pyramidal tract injury can contribute to clumsy behavior. We found that partial lesions spared most of the movements that are compromised by complete lesions, including limb posture, placing responses, limb preference in reaching for food, and success in food retrieval. Nevertheless, rats in both groups displayed enduring deficits in aiming the paw to advance it toward the food, in supinating the paw to retrieve food, and in posture. The deficits appear to derive from an inability to perform fixations, movement requiring complementary actions in body segments. Accordingly, it is suggested because even partial lesions can impair fixations, clumsy behavior in humans might be due to pyramidal tract damage or dysfunction. This finding could be relevant to the development of specific remedial training in fixations to improve movement skills.

Coordinated behavior requires two separate forms of fixation. External fixations involve directing a body part to a target and maintaining opposition to the target even though it may move, as occurs when a playing animal maintains its snout on a body target, such as the neck or hip of its partner (Golani & Moran, 1983; Yaniv & Golani, 1987). When the partner moves, the targeting animal must also move to maintain the opposition between its snout and the target. If the partner escalates its movement, so to must the targeting animal escalate the size of its own movements to maintain opposition. Internal fixations are those in which a segment of the body is fixed while other body parts move, as occurs when a magpie holds an object with a foot while the head moves to take the object with the beak (Pellis, 1983) or as a human holds an object in the hand while the head moves so that the object can be grasped by the mouth (Whishaw et al., 2002). For the transfer to be successful, the position of the foot or hand must maintain its spatial location, thus compensating for the movement of the head. With these two forms of fixation in mind, one can conceptualize two forms of clumsy behavior: one in which a target is missed, which would constitute a failure of an external fixation, and the other in which a target is reached but movement is inefficient or bizarre, which would signify a failure of an internal fixation.

Pyramidal tract lesions appear to produce clumsy behavior of the second type in which internal fixations are compromised (Whishaw et al., 1993). For example, the animals can still locate and identify food and extend a limb to grasp food but their movements are abnormal. This impairment in internal fixation follows both complete and partial lesions. After partial lesions, an animal's success scores are at control levels but its reaches are unusual and characterized by may additional body adjustments. For example, to aim the limb, a control rat first adducts the lower arm so that the tips of the digits are aligned with the midline of the body. From this 'aiming' position the limb is easily directed through the slot to the food. To obtain alignment, a rat must hold the digits at the midline of the body when the elbow is adducted. For this to occur there must actually be a compensatory movement of abduction of the lower arm as the upper arm is adducted (Whishaw & Pellis, 1990). Typically, the rats with both large and small pyramidal tract lesions failed to adduct the arm so that the digits were aligned with the midline and they further abduct the lower arm as the upper arm is adducted. This movement leaves the limb in a peculiar posture with the 'elbow in' and the 'digits out' rather than with the forearm aimed for the slot. Additionally, these movements are not performed as discrete actions of the limb but are assisted by rotations of the body. A second example of impairment in fixation is seen when an animal with a pyramidal tract lesion attempts to take food from its paw with its mouth. The paw 'moves away' as the mouth approaches. That internal fixations are sensitive to pyramidal tract lesions suggests that a function of the pyramidal tract is to assist in enabling internal fixations.

Given the findings of the present study and the nature of the impairment that follows pyramidal tract lesions, it is possible to suggest that some forms of clumsy behavior in children can be related to pyramidal tract damage. That is, a child might be able to identify a target and might be able to obtain that target but the movements that the child uses in doing so might be unusual and thus classified as clumsy. The pyramidal tract is an especially interesting substrate for clumsy behavior in that studies on developing animals suggest fixations must be learned (Pellis, 1983). Thus, clumsy behavior would emerge as a failure in learning new skills. It is possible to suggest that as the pyramidal tract is plastic (Schreyer & Jones, 1982; Terashima, 1995; ZíGraggen et al., 1998), impairments in fixations in this form of clumsy behavior could be identified and remediated by specific training in fixations rather than in more global training in coordination.

The size of the small lesions used in the present study included less than one half of the pyramidal tract as determined by measures of the area of the tract at the level of the lesion. Thus, the small lesions were substantially different in size from the large lesions that were relatively complete. The measure of lesion size might have underestimated the size lesions somewhat as the remaining tract could have expanded into the cavity produced by the lesion. The lesions also varied in their mediolateral location, but irrespective of location, the behavioral deficits that they produced appeared to be similar. The mediolateral placement of the lesions might not be critical as the results of a number of studies show that at the level of the medullary pyramidal, the topographic organization of the fibers with respect to their cortical origin is lost (Barnard & Woolsey, 1956; Wise et al., 1979). Despite the variation in size and placement, the partial lesions produced In the present study seem appropriate for determining which aspects of behavior are spared and which aspects of behavior are compromised by partial lesions.

A surprisingly large number of measures of contralateral forelimb use typically compromised by large lesions were insensitive to the small lesions. Such measures included adduction of the forelimb to the ventrum of the body when the rat was suspended by the tail, contact placing, limb preference in reaching for food, and success in reaching for food in both simple and demanding skilled reaching tasks. Thus, all these measures appear to be sensitive to only very large lesions of the pyramidal tract. Noteworthily, these are the measures of forelimb use that can be most easily and objectively scored. Accordingly, they might also be measures that can be expected to be sensitive to procedures that produce sparing or recovery of the pyramidal tract after injury (Terashima, 1995; Weidner et al., 2000).

Nevertheless, whereas the group with large pyramidal tract lesions displayed impairments in posture and an impairment on almost all qualitative components of the reach, qualitative impairments were observed in rats with small lesions. The qualitative impairments small lesion group were most obvious in posture, in which the rats persisted in using a diagonal approach to the slot through which they reached for food, in aiming the limb through the slot, and in supinating the paw to place food in the mouth. Noteworthily, these movements are also those that are the most obviously affected by large pyramidal tract lesions.

It is possible that sparing on the quantitative measures of behavior was observed in rats with small pyramidal tract lesions because by the time the tests were administered, the rats had undergone substantial recovery. For some measures of reaching this happened some weeks after surgery. Such recovery could have been mediated by fiber sprouting within the pyramidal tract (Schreyer & Jones, 1982; Terashima, 1995; ZíGraggen et al., 1998). This possibility was investigated by first training rats on the single pellet reaching task and then examining their quantitative and qualitative performance on the day following partial sections of the pyramidal tract and then again at 14 days following surgery. The rats with the pyramidal tract lesions displayed no impairment in success on any day following surgery. On the day after surgery, they did display qualitative deficits that persisted for all 14 days of testing. Because any recovery observed following the lesions would be expected to be complete by 14 days (Whishaw, 2002), the results suggest that he behaviors spared or comprimised by partial lesions are not modified greatly by the processes of recovery.

In summary, certain investigators have associated the function of the pyramidal tract with independent movements such as those exemplified by the movements of digits when an object is grasped. For this reason, the same investigators have suggested that the pyramidal tract has unique functions in primates. In contrast, the results of the present study (see also Whishaw et al., 1993; Whishaw & Metz, 2002) suggesting that the pyramidal tract is important for internal fixations provides a possible function for the pyramidal tract in all species in which it is found. The suggestion presented here also opens up new avenues of investigation into the possible roles played by the pyramidal tract in many kinds of skilled movements, which when impaired would be described as clumsy acts. These avenues or research would direct investigators from a narrow focus on digit movements to a more general consideration of how coordinated movements are learned and performed.

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