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The structure of skilled forelimb reaching in the rat: a proximally driven movement with a single distal rotatory component

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The movements of rats trained to reach through an aperture for food pellets, located on a shelf, were videorecorded and filmed from lateral and ventral perspectives for analysis using Eshkol-Wachman Movement Notation (EWMN). Reaching was subdivided into phases of locating the food and advancing the limb to grasp the food, bringing the food to the mouth, and returning to the starting position. Further analysis of the movements comprising these acts revealed a number of novel findings. (1) Most of the first phase of the movement is produced proximally, with the limb lifted, aimed, and advanced from the shoulder. (2) After the limb is lifted from the substrate to initiate reaching, it is carried to a parasagittal position so that the long axis of the forearm is aligned along the midline of the body. This aspect of the movement 'aims' the limb toward the target. (3) The digits are opened as the limb is advanced from the aiming position toward the food. As the paw approaches the food, pronation of the palm is accomplished by abduction of the upper arm. (4) As the limb is retracted, the digits are closed to grasp the food. As retraction ends, the paw is supinated by a rotatory movement at the wrist. This is the only distal rotatory movement. (5) The position taken by the second forelimb, as it is adducted to aid in holding the food pellet for eating, resembles the 'aiming' posture. The results are discussed in reference to the kinematics, neural control, and the evolutionary origins of reaching in the rat and other animals. Additionally, the results provide a framework for analysis of changes in movements produced by physiological manipulations.

INTRODUCTION

Since Peterson's[18] early experiments, directed toward establishing cortical localization of limb use, rat reaching has been adopted as a model system to analyze the development and lateralization of motor control, functional recovery after brain damage, and the neural control of skilled movement (see refs. 3, 20 for reviews). Some more recent studies have begun to consider, more generally, the place that rat skilled forelimb use has in the evolution of skilled limb use in mammals. To date, this work has shown that rat reaching differs from reaching by primates in two important respects. First, it is guided by olfaction rather than vision[22]. Second, it has been described as stereotyped because it has much the same form in many test situations, including reaching through slots, into tubes and into trays[1]. What has limited both functional analyses of reaching and species comparisons, however, is a lack of information about the details of the actual reaching movement. To date, analysis has been limited to recording either the success of the

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movement in obtaining food or the speed and trajectory that the paw takes during advancement to, and retraction with, the food.

The purpose of the present study was to examine and describe the details of the reaching movement of the rat. To obtain a reliable representation of the movement, the behavior was first videotaped and filmed so that frame-by-frame analysis of movement components could be made. The components of the movement were then described in terms of relations and changes of relation between parts of the body using the Eshkol-Wachman Movement Notation (EWMN) system[4,5]. This analysis permits the isolation of the elementary building blocks of the movement and aids in conceptualizing the rules of their sequencing. For this analysis, the building blocks of movement are represented by EWMN signs. Relevant components of the movement were then represented graphically. This analysis not only presents an accurate description of reaching but also provides examples of how important features of the movement can be graphically represented.

MATERIALS AND METHODS

Subjects

Eight adult female Long–Evans hooded rats, weighing between 200 and 230 g when the study began, were used. They were housed in hanging wire mesh cages in an animal colony lighted on a 12 : 12 h light–dark cycle. Testing was done during the light portion of the cycle. The rats were food-deprived to 90% normal body weight and received once-a-day supplemental feeding of measured amounts of food to maintain deprivation.

Apparatus

The entire testing apparatus was made of clear Plexiglas so that the rats could be filmed from any direction. The floor of the test apparatus was 27.5 cm by 30.5 cm and mounted on a 45-cm high pedestal. There was a 15-cm high wall at the front of the stand. In the center of the wall a 1.2-cm wide and 10-cm high aperture was cut, through which the rats could reach for food. On the outside of the wall, mounted 3 cm above the floor, was a 3.5-cm by 4.5-cm shelf. Food pellets were placed in one of two small indentations on the floor of the shelf. The indentations were 1.3 cm away from the inside wall of the shelf and were centered on the edges of the slit through which the rats reached. On the stand, two Plexiglas walls, separated by 10.5 cm, made an alley to the aperture through which the rats reached. The walls ensured that the rats aligned their body with the aperture when they reached (Fig. 1).

Food

The rats reached for round 190-mg Rodent Chow food pellets (Bioserve Inc., Frenchtown, NJ).

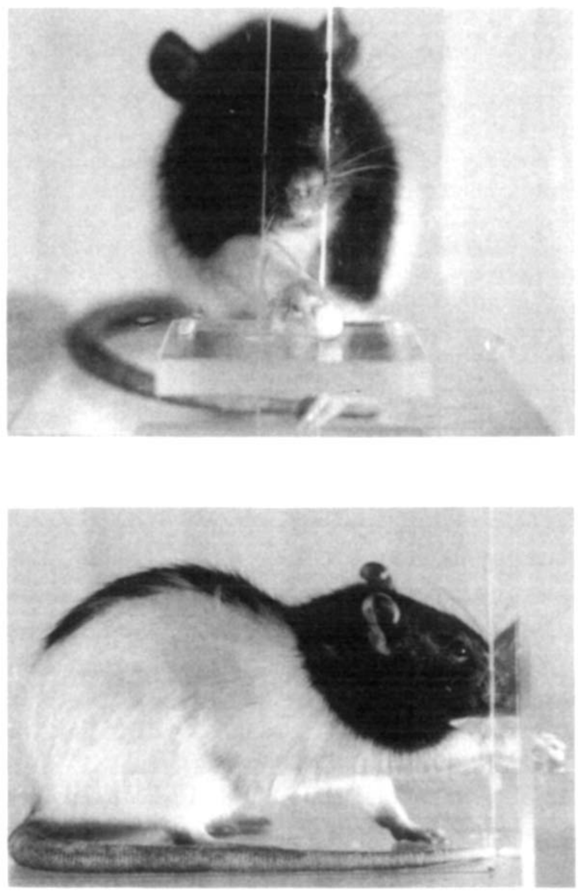

Fig. 1. Test apparatus. A food pellet is placed on the shelf. To obtain food the rat reaches through an aperture. Since the apparatus is clear, the rat can be filmed from either lateral or ventral perspectives.

Videorecording and filming

Videorecords were made with a Sony Video 8 CCD-VII portable camera with shutter speed options of 50, 100, 500, 2000 and 4000 feet per second. Illumination for high shutter speed filming was provided by a two-arm Nikon Inc., MII cold light source. The film from the Video 8 was copied onto a Betamax format tape for analysis. Frame-by-frame analysis at 30 frames per second was provided by a Sony Super Betamax GCS-50 recorder.

Filming was done with a Bolex camera set at 64 frames per second, using Eastman Ektachrome video news color 7240 tungsten film. The frame-by-frame film analysis was done with a Lafayette motion analyzer.

Procedure

The rats were food-deprived and then given a measured amount of food each day until they were reduced to about 90% of their initial body weight. After training began, feeding was restricted so that the food obtained during training/testing plus supplemental feeding maintained them at this weight. Training lasted for about an hour each day for two weeks. For the first week of training, the rats were placed in boxes (10 × 18 × 10 cm high). They were able to reach through metal bars (separated by 9 mm) to obtain food from trays mounted on the front of the boxes[19]. Once the animals were reaching for food they were transferred to the test apparatus for further training. In the test apparatus, one food pellet was placed in the food receptacle contralateral to the rat's preferred limb. (Because of the way the paw is pronated to grasp food (see below), effective reaching cannot be obtained when the food is in the ipsilateral food receptacle.) The food pellet was replaced after the rat either grasped it or knocked it off the shelf. Each rat was given about 20 food pellets each day. All of the rats were reaching and obtaining food after a week of training.

Tests

Each rat was given two videotaped tests during which they reached for 20 food pellets. In the first test the rats were videotaped from the side and in the second test they were videotaped from below. Three rats were filmed. A total of 300 ft of film was used for the lateral view and 300 ft of film was used for the ventral view. The film provided about 20 complete reaching sequences from each perspective.

Behavioral analysis

Two different types of behavioral analyses were used. The first analysis used a conceptual framework derived from EWMN[5]. This notation system has been adapted for the study of animal motor behavior[8]. 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 articulated axes (i.e. body and limb segments). A limb is any part of the body which either lies between two joints or has a joint and a free extremity. These are imagined as straight lines (axes), of constant length, which move with one end fixed to the center of a sphere. The body is represented on a horizontally ruled page. Each horizontal space represents a part of the body. Vertical lines divide the manuscript page into columns which denote units of time (e.g. frames of a film). The signs for movement are read from left to right and from bottom to top. An important feature of EWMN is that the same movements can be notated in several polar coordinate systems. The coordinates 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, invariances in that behavior may emerge in some coordinate systems but not in others. Thus, the behavior may 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[6,7,8,16]. In this study, reaching sequences were notated from the lateral view, hence giving only vertical movements, and from the ventral view, hence giving only horizontal movements. Juxtaposing these views gave a complete analysis of the movements involved.

Once the topography of the reaching movement was established by EWMN, a number of aspects of the movement were measured and documented using a Cartesian coordinate system with initial and terminating components of the movements as reference points.

RESULTS

Components of reaching

We divided reaching into three parts as summarized in a simplified EWMN score shown in Fig. 2. *(1). Orienting toward and reaching for the food pellet.* To orient, the rat raises its head until the snout is poked through the food aperture. Then, the whole body is shifted forward, by pushing with the hindlegs, and the rats sniffs the food pellet. These movements are achieved with or without either of the forepaws being in contact with the floor. This is then followed by reaching and grasping. The head is raised during reaching, sometimes accompanied by a lordotic movement of the back, to allow the forelimb to advance to the food pellet. *(2). Bringing the food pellet to the mouth.* To bring the food pellet to the mouth, the limb is retracted and the palm is supinated so that it faces the anterior side of the mouth. At about the same time the head is withdrawn, sometimes accompanied by arching of the back, so that the snout is retracted from the food aperture, with the limb being carried passively with it. The other forelimb is then usually raised to aid in holding the food during eating, or continues to support the forequarters as in the example illustrated here. *(3). Readjusting the body and limb position after completion of the task.* To readjust posture, the body is shifted backward, the forelimbs are placed onto the ground, and the head is raised to its starting position.

Movement description

A detailed notation score of a single reach, obtained from a videorecording of the lateral view

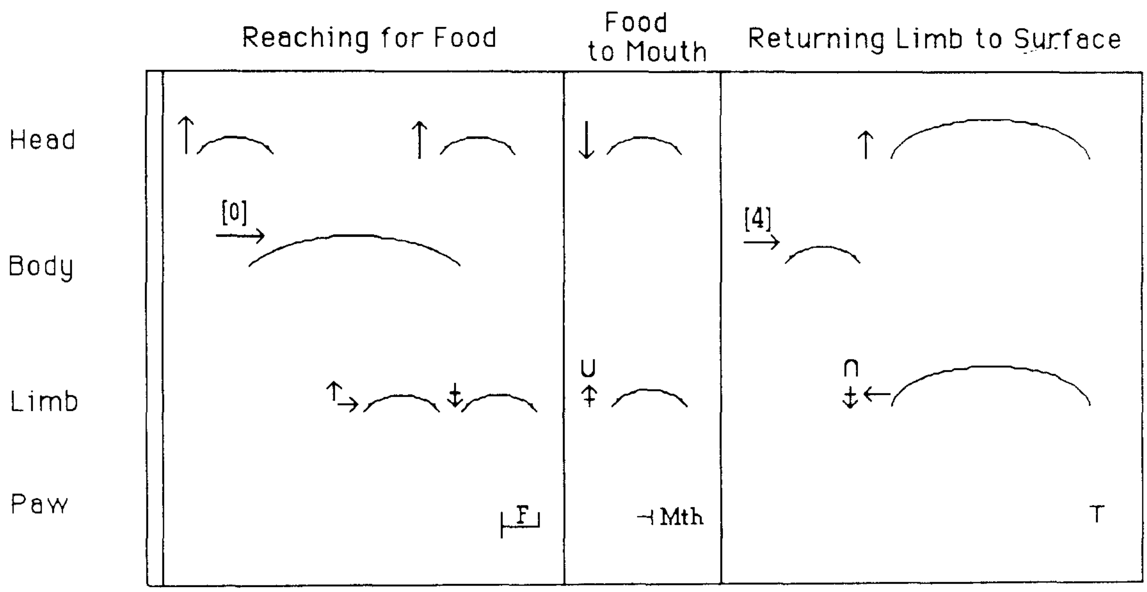

Fig. 2. A summary of a EWMN motor score of a single reach. The movement is broken down into three phases, reaching for food, bringing the food to the mouth, and returning to the initial position. The movements of the head, body, limb, and paw are indicated during each of these phases. Arcs indicate the relative durations of the movements. In the first phase the head is lifted (↑), the body is shifted forward ([0]), the limb is brought in toward the body to point toward the food (↑→), the head is raised and the limb extended toward the food (‡), and the paw grasps the food pellet (F) shown by the sign ⊢. In the second phase, the head is lowered (↓) and the limb is retracted (†) and rotated (∪) so that the paw faces medially to contact (⊣) the mouth (Mth). In the third phase, the body is shifted backward ([4]), the head is raised, and the limb is rotated (∩) so that the paw faces ventrally so that the palm contacts the floor (T). ↑,↓, clockwise and counterclockwise vertical planar movement; ←,→, clockwise and counterclockwise horizontal planar movements; ∩ ∪, clockwise and counterclockwise rotatory movements; †, flexion; ‡, extension; ⊢, grasp; T, weight bearing contacts with the ground; ⊣, other contacts.

	1	2	3	4	5	7	8	9	12	13	14	15	16	18	19	20	23	24
Hd/Nk	(1H)	↑		Sniff				↑		(2)	↓	(1)				↑		(1H)
Mouth												⊣6			=			
Torso	(2)				(f2)													
Right Forelimb																		
Upper	(5)																	
Lower	(6) T̄					=		(4)										
Paw	T																	
Left Forelimb																		
Upper	S					↑	(1H) (→)	↑		(2)	↓	(1H)				↓	(4) (←)	
Lower	(4)							↓			∪ ↑	(2)				∩ ↑	(4) (5)	
Paw	T					(P) =			M ‡	‡ F		⊣ 0			(P) =	m ‡	T	
Weight					[0]								[4]					

Fig. 3. A detailed EWMN motor score of a single reach. The numerals on top indicate the frames from the videorecord (30 f/s). The first left column on the score describes the initial position of the rat. Symbols: T̄ light contact with the ground without body support; S, symmetrical position for homologous side of body; (→)(←), horizontal movement, since this notation score is for vertical movements only, these horizontal movements are represented as positions for the limbs and hence are enclosed in parentheses; P, passive movement (digits dropped into partially flexed position); =, loss of contact, F, food pellet, f, fixation, i.e. means that the body segment maintains a constant relationship to space; (2), vertical position for that limb (that is, the number represents the vertical position on the EWMN sphere and the dash represents the missing horizontal position, since from the lateral view only vertical movements were visible), (4), rotated state for the limb (that is, the side of the body or limb segment facing vertically upward); [0], [4], forward and backward shift of weight, which in this case involves whole body displacement with the limbs maintaining contact with the ground; ⊣ 0 or ⊣ 6, contact with that aspect of body surface, 0 ventral surface, 6, left side; M/m, maximum and minimum movement; 1 unit is 45°; H, one half a unit; Hd/Nk, head and neck. Movement obtained from videorecord, 30 f/s. For further details on reading the EWMN score see Eshkol, 1980; Ganor and Golani, 1980; Golani, 1976.

of the rat, is shown in Fig. 3. Movements of a number of body parts and limb parts were described independently. These include the head and neck, mouth and torso, and the upper limb, lower limb, and paw of both the right and left forelimb. Movements of each body part are documented across successive videoframes. This analysis reveals detailed features of the reaching movement, including aiming, reaching and pronation, and withdrawal and supination.

Aiming. The initial lifting of the reaching paw off the ground is achieved by raising the upper arm. Once lifted off the ground (frame 8), the paw and elbow are carried inward, toward the parasagittal plane, by adduction of the upper arm. These movements orient the limb so that the paw is located just below the mouth and the long axis of the forearm is aligned along the midline of the body. This movement appears to 'aim' the paw at the pellet. What is noteworthy about this aspect of the movement is that the paw does not move directly toward the pellet, but is first moved with the forearm toward the midline to take up the aiming position.

Reaching and pronation. Once the limb is in the aiming position, it is advanced toward the food pellet (frame 10). This movement is distinctive in two respects. First, it is rapid in relation to preceding movements. Second, the digits, which have been in a semiflexed position to this point, begin to open as the limb is moved forward. Toward the end of the forward movement of the limb, the upper arm is abducted and this movement pronates the palm over the food. The digits extend fully during pronation.

Withdrawal and supination. As the limb is retracted, the digits close, thus grasping the food (frame 11). During the initial portion of retraction the limb maintains its parasagittal orientation but toward the end of retraction the forepaw is supinated so that the palm, holding the food, is turned toward the rat's mouth. Supination is produced by a movement at the wrist. Once the limb is withdrawn it is held immobile for a brief period as the head is lowered so that the mouth contacts the food (frame 13). The rat then sits back, carrying the limb passively. Once the rat is in a sitting position, it transfers the food from the paw to the mouth. The limb is only counter-rotated to its initial position as the paw is replaced on the ground and this is accomplished in part by abduction of the upper arm.

Trajectory of the limb from a lateral view

Some representative frames of a reach drawn from film of a lateral view are shown in Fig. 4. Movements of the snout to sniff the food are shown in frames 1–8, movement of the paw to grasp the food are shown in frames 8–18 and retraction of the paw is shown on frames 18–31.

The path taken by the snout and the tip of the paw during a reach is shown in Fig. 5. For the extension phase of the movement, the path of the nose is shown by open circles connected with dotted lines and the path of the paw is shown by solid circles connected with solid lines. For the retraction phase of the movement, the open and closed circles are not connected. This Cartesian

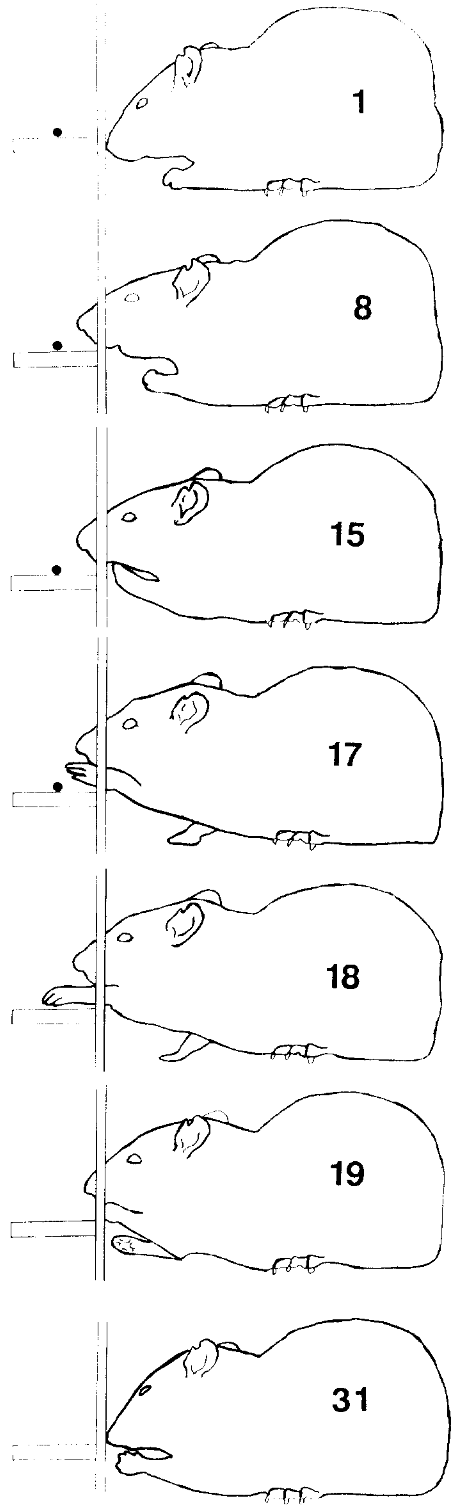

Fig. 4. Lateral view of a reach. Movement of the snout to locate the food (frame 1 to 8), extension movement of the limb (frame 15 to 18), retraction (frame 18 to 19), and eating (frame 31). Film, 64 f/s.

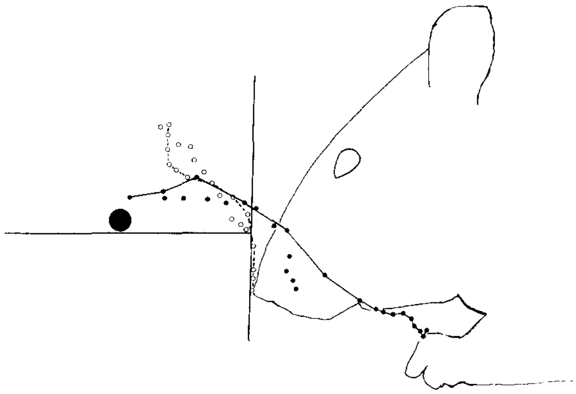

Fig. 5. Path taken by the snout and the paw during a reach. Path of the nose is shown by open circles and path of the paw is shown by closed circles. Extension phase of the movements are indicated by dotted and solid lines. Circles are not connected for the retraction phase. Note that the reach follows the initial curve of the snout. Film, 64 f/s.

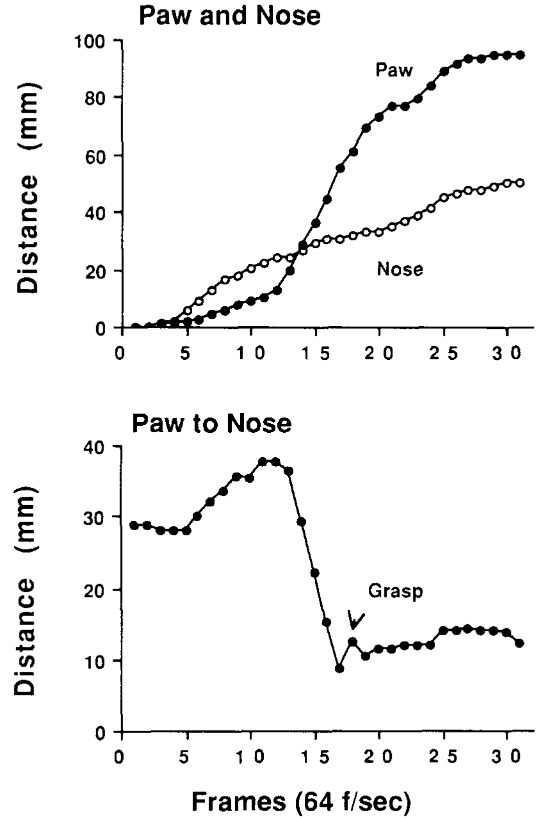

Fig. 6. Cumulative curves of movement distance for the paw and nose (top) and their relative distances (bottom). Note that the movement of the nose precedes the movement of the paw.

reconstruction of the movement illustrates two things. First, the movement of the paw follows the movement of the snout during the third quarter of the extension movement. Second, the extension movement carries the paw in an arc above the food and then down onto it, with the upward phase of the movement apparently being more rapid than the downward phase.

The movement of the paw and nose and the relation between these two body parts are graphically represented for a single reach in Fig. 6. The top portion of Fig. 6 shows the cumulative distance moved by the paw and by the nose. Here it can be seen that the two movements appear to occur in three phases. First the nose is moved. This is followed by a rapid movement of the paw as it advances to grasp the food, and then both body parts move almost together as the rat sits back to adopt a sitting position from which to eat the food. The relation between the two body parts is illustrated in the bottom portion of Fig. 6. Here it can be seen that the distance between the nose and paw initially increases as the nose is oriented toward the food. Then the distance between the two first rapidly decreases and then slightly increases as the limb is advanced past the nose to grasp the food. Finally, there is a slight decrease between the paw and nose as the paw brings the food pellet to the mouth.

Trajectory of the limb from a ventral view

Some representative frames of a reach drawn from a ventral view are shown in Fig. 7. In frame 9, the rat has directed its snout toward the food. In frame 14, the limb has been brought toward the midline of the body to aim at the food just prior to extension to grasp the food (frame 17). Frame 38 illustrates a typical eating posture with both limbs drawn into the parasagittal plane to hold the food for eating.

The path taken by the elbow and the paw during a reach for a ventral view is shown in Fig. 8. For the extension phase of the movement, the path of the paw is shown by closed circles connected with a solid line and the path of the elbow is shown by open circles connected with dotted lines. For the retraction phase of the movement, the closed and open circles are not connected.

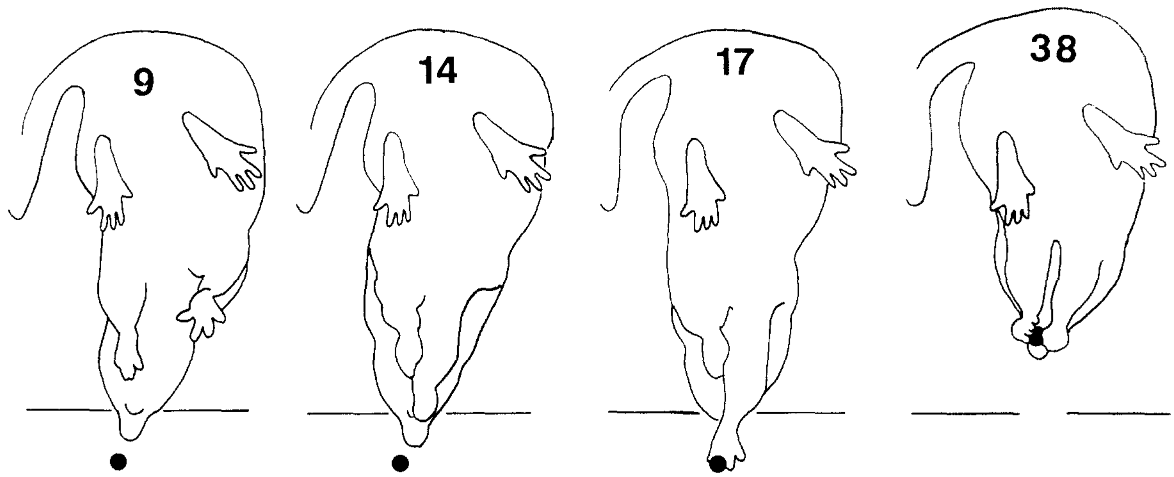

Fig. 7. Ventral view of a reach. Movement of the snout to locate food (frame 9), parasagittal movement of the limb to aim the paw at the food (frame 14), grasp (frame 17), eating (frame 38). Film, 64 f/s.

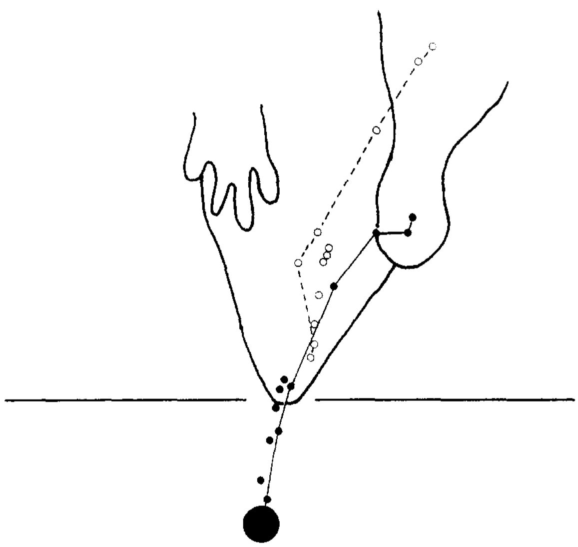

Fig. 8. Path taken by the paw and elbow during a reach. Path of the paw shown by closed circles and path of the elbow is shown by closed circles. Connected points show the extensor phase of the movement and unconnected points show retraction. Film, 64 f/s.

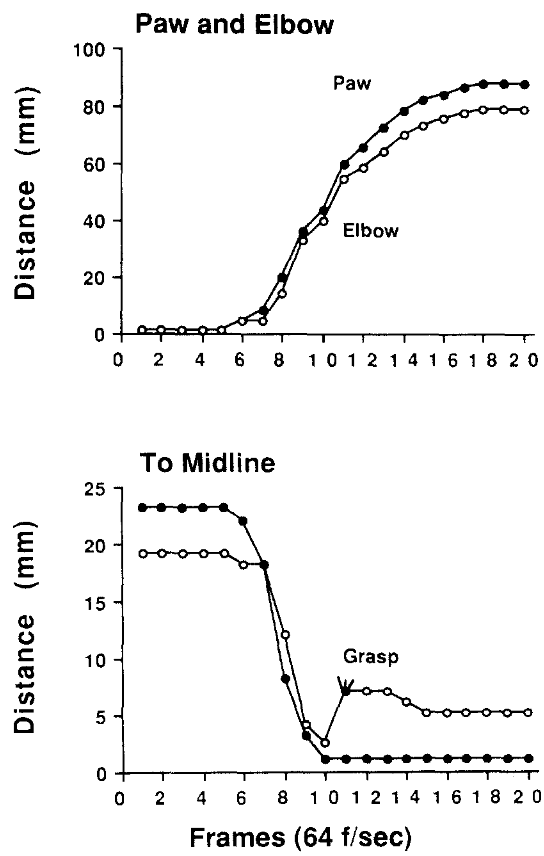

Fig. 9. Cumulative curves of the movement distance of the paw and elbow (top) and their relative distance to the body midline (bottom). Note that the paw and elbow are oriented to the midline before the extensor phase of the reach occurs.

This reconstruction illustrates the movement of the paw and elbow into the parasagittal plane preceding the rapid advancement of the limb and also illustrates that this position is retained during retraction of the limb.

The movement of paw and elbow and the relation between these two body parts and the midline of the body are graphically represented for a single reach from a ventral view in Fig. 9. The top portion of Fig. 9 shows the cumulative distance moved by the paw and elbow. Here it can be seen that the movements are synergistic. The relation between these two limb parts to the midline of the body is shown in the bottom portion of Fig. 9. It can be seen that the movement of the forelimb to the parasagittal plane occurs in the initial portion of the reach and precedes the extension of the limb to grasp the food. The abduction of the upper arm to pronate the paw to grasp the food is also apparent just prior to food grasping.

Stereotyped features of reaching

The generality of the description of the overall reaching movement was evaluated by examining 10 successive successful reaches from each rat. We scored each reach in terms of whether the following movements were apparent as described by the EWMN analysis: aiming, digit opening during advancement of the limb, palm pronation by upper limb abduction, grasping during retraction, and supination of the palm by rotation at the wrist. Each of these movement components were indistinguishably present in every reach.

DISCUSSION

Previous studies of limb use in the rat have characterized the movement in terms of end points, success or failure, or in terms of a Cartesian trajectory of the paw toward the target. The present study describes the movement in terms of relations between limb segments, other body parts and the target. This study documents a number of features of this movement. (1) The limb is positioned and advanced by movement of the upper arm, (2) the limb is first 'aimed' by being moved into a parasagittal position beneath the body, rather than being moved to the target directly, (3) the palm is pronated by abduction of the upper arm, (4) the only rotatory distal movement is at the wrist to supinate the palm to present the food to the mouth on retraction, and (5) the aiming posture from which the reach is initiated resembles the posture of the forelimb when holding food during eating.

A major limitation in using Cartesian trajectories to identify regularities in a sequence of complex movements, such as reaching, is that the trajectory of one body part, such as the paw, may result not only from its own movements, but also from the movements of other body segments. The EWMN is ideally suited to disentangle such simultaneous movements as it distinguishes between cases of movement by the body segment itself and cases where the body segment is carried along by adjoining segments. For example, the trajectory of the snout during reaching in aiming and grasping phases is produced by an initial head and neck movement, so that the snout pokes through the slot, followed by continued movement of the snout forward by the hindlegs pushing the body forward, with the head finally raised further upward by a lordotic movement of the back. Thus the Cartesian trajectory of the snout is produced by a composite set of movements involving the head, neck, body, and hindlegs. Depending on the distance from the slot at the outset of the reaching movement, a relatively stereotyped snout trajectory can be maintained by compensatory movements of these and other body segments. Similarly, although a Cartesian trajectory can describe the path of the paw to the food target, an EWMN analysis shows that the movement is produced by proximal movement of the shoulder and that the limb is 'aimed' before it is finally advanced toward the target. Thus, EWMN analysis provides precise description and enables the range of compensatory movements by each body segment to be demarcated[8,17]. Alternatively, the body segment(s) responsible for the disruption of the 'normal' trajectory can be identified (see below). Cartesian trajectories become more powerful tools for the descriptive analysis of movement patterns when coupled with an EWMN score sheet that enables one to causally identify the body segments responsible for each phase of a trajectory.

One of the useful features of EWMN analysis is that it aids in the identification of features of movement that might be missed using a more global approach. Once relevant features of a movement are isolated, however, they can be documented using less demanding behavioral methods. For example, once we identified the major movements that comprise a reach we could quickly confirm that these were typical of all reaches made by all rats in our task. But at the same time, we do not imply that this is the only way that rats can reach for food. In very different situations the movements that they make could be different and here EWMN could again be useful for comparative purposes. Nevertheless, given that most reaching tasks require a rat to reach through an aperture to get food, it is very likely that the pattern of movements that we describe here will be the movement pattern that is used.

The graphic representations of reaching in this paper have been made to facilitate the analysis of limb use following physiological manipulations, such as might follow damage to various central motor areas. Again, typical analyses of these impairments have been directed toward describing end point performance, such as numbers of reaches and hit percent. We have examined a small number of rats that had received motor cortex or striatal lesions. The animals displayed distinctive abnormalities in the qualitative aspects of the movements. The following examples will serve for purposes of illustration. After motor cortex damage, rats miss food when they reach and they have difficulty bringing the food to their mouth[2,20]. The present analytical procedures indicate that their impairment is not in advancing and retracting the limb, but in pronating and supinating the paw. This explanation of the impairments is consistent with evidence that suggests that the motor cortex is involved in the production of rotatory joint movements[13–15]. On the other hand, rats with striatal damage have no apparent deficit in pronation and supination but are deficient in their ability to advance the limb. This result is consistent with a suggestion that the striatum is involved in ramp movements[12]. Many of the apparent abnormalities that the brain-damaged rats display as they attempt to reach are actually compensatory movements that enable them to succeed in spite of their deficits.

There have been two suggestions concerning the origins of skilled forelimb reaching. Grillner and Wallen[10] have suggested that reaching evolved from forelimb stepping. Brácha et al.[1] suggest that reaching evolved from digging movements. A complete evaluation of these ideas requires a description of stepping and digging that is analogous to that described here for reaching. Currently this is not available. We have made a few preliminary observations of walking and digging. Neither movement, however, involves a similar parasagittal movement of the forelimb prior to extension, pronation by abduction of the upper arm, or supination by wrist rotation. Thus, they both differ significantly from reaching.

Our description of the reaching movement provides an alternative explanation of the origins of reaching. Usually, rats pick up food with the mouth and then sit back and transfer the food to the forepaws to eat it[20]. The movements of the forelimbs to grasp the food resembles the initiating parasagittal movement of the forelimb in reaching. Thus, this initial aiming movement of the limb may have its origin in food holding. Furthermore, in the present analysis, we noted that the extension component of a reach follows the orienting movement of the snout toward the food. In a sense, it appears that the limb comes forward to grasp an object that is proximal to the snout. Thus, this component of the movement also has the appearance of developing from a movement that involves hand–mouth food manipulation. In considering the origins of these components of reaching, it is interesting that rats with no neocortex can transfer food from the mouth to the paws in a seemingly normal fashion[20]. This suggests that some of the neural control of the movement, notably the aiming component, is organized subcortically.

In summary, this EWMN analysis provides a number of novel findings concerning movements used by rats when reaching. It also provides a number of novel suggestions concerning its neural organization and evolution. Additionally, many features of rat reaching, including aiming, paw trajectory during extension and retraction, and the rotatory movements that orient that paw seem similar to human reaching[9,11]. This suggests that major features of mammalian skilled limb use were established early in evolution and their genesis can be examined fruitfully in the rat.

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