

Research report

Skilled forelimb reaching for pasta guided by tactile input in the rat as measured by accuracy, spatial adjustments, and force

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Abstract

Rats are capable of reaching for food with a single forelimb, but since they locate the target of their reach using olfaction, it is unclear how they adjust their limb movement to compensate for errors. Although it is thought that their reaching movement is ballistic and can only be adjusted by trial and error, whether they can use haptic cues to aid in locating and identifying a target has not been examined. The present study addressed this question by allowing rats to reach through a slot for rigidly held pieces of uncooked pasta of varying thickness, which could be oriented vertically or horizontally from different points around the slot and which were attached to a force transducer. The tasks required that animals not only adjust their reach and grasp to the target's location but also identify the target based on its texture. Acquisition curves were made of head orientation, limb transport trajectories, number of attempts per success, paw orientation, breaking direction and force of the grasp. A haptic discrimination test used pasta and similar sized metal rods with different tactile properties as discriminanda. The results indicated that whereas postural orientation and limb transport trajectory were not modified as a function of target orientation, paw orientation and grasp force did vary as a function of the sensory qualities of the target object, and the rats could make a haptic discriminative choice of a target object. The results show that the rat is capable of adjusting paw movements using haptic information, suggesting that somatosensory features of sensorimotor control of limb and paw movements in carnivores and primates are shared by rodents. This commonality points to a conservation of motor control in mammals, explains some of the idiosyncratic features of rat reaching behavior, and confirms that rodents provide a good model for investigating sensorimotor functions. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Since Peterson's [21] seminal description of skilled reaching in the rat, the species has been used for a wide range of studies on the neural control of skilled movements [4,6,7,29] as well as for studies on the evolutionary origins of skilled movements [32,37]. In the course of these studies, tasks have been developed in which animals reach through slots [25], onto shelves of different heights [18], down onto staircases [19,35], onto

moving conveyor belts [8] or turntables [13] for food. Their forelimb use in handling natural food items [37] as well as prey items [10] has also been examined. The neural control of their skilled forelimb movements is very similar to that used by carnivores [1] and primates [15] in that a variety of neural structures including motor cortex [3,9,12,20,30], the pyramidal tract [34], rubrospinal tract [33], basal ganglia [5,29] and dorsal column of the spinal cord [17] all contribute to limb movements and success. Detailed analyses of the movements displayed in various tasks, and the changes undergone in those movements as a result of brain manipulations, suggest that the rat has a basic reaching movement that undergoes slight modifications in differ-

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ent tasks. They retrieve the item with the mouth or paw as the task demands [36], they use an elbows-in posture for reaching and holding [19,25,31], and they use a variety of digit movements and postures for grasping and holding objects [24].

Although there are similarities in skilled forelimb use between rodents, carnivores and primates, rodents display a striking difference in sensory control in that they use olfaction [28] rather than vision to identify a food object and its location. Furthermore, if they are reaching for a food item with a forepaw, after first identifying the item olfactorily, they must then displace their nose from the target in order to advance their limb to grasp it [28]. Thus, in large part their reach must be preprogrammed and executed without on-line sensory guidance. It is perhaps for this reason that animals seldom obtain an object on the first reach and even with extensive training only obtain a target object on $\sim 75\%$ of reaches. Because their reaches are preprogrammed, rats may be constrained to execute a number

of reaches in order to calibrate a reach trajectory and grasp that will be successful. For these reasons, it has been generally assumed that a rat's reaches are ballistic and thus sensorially unmodifiable [2,38], but this proposition has never been explicitly examined.

The purpose of the present study was to examine whether the rat can modify components of its reaching movements using sensory feedback obtained during the reach itself. The animals were trained to reach through an aperture for a piece of uncooked straight pasta that was anchored at one end in varying orientations behind an aperture. The animals' accuracy and modifications of the reaching movement were examined using high-speed videorecording, frame-by-frame video analysis, and Cartesian reconstructions of actions from a digitized record of the movements. In addition, the animals were given discrimination problems in which they were required to distinguish between pasta of varying size, pasta and a similar size and textured metal rod, and pasta and a differently textured metal rod. The target items were also held in a force transducer in order to determine whether qualitative features of the target influenced the torque and force applied in breaking the pasta free from its anchor. All of the results were analyzed with the objective of identifying the sensory constraints on the rat's reaching movements.

2. Materials and methods

2.1. Subjects

Animals used were eight adult, female, Long–Evans rats weighing ~ 250 g when the study began, and were housed together in wire mesh cages in a room maintained at a temperature of $\sim 22^\circ\text{C}$ and on a 12:12-h light-dark cycle, with lights on at 08:00 h. Prior to the beginning of the experiments, the rats were placed on a restricted food schedule that reduced their body weight to 95% of normal body weight. During initial training, they were given supplemental feeding to maintain body weight but once they had acquired the task, they were fed ad libitum.

2.2. Reaching task

The animals reached for pieces of pasta in a box constructed of clear Plexiglas (Fig. 1A). The box dimensions were 12 cm wide by 40 cm deep by 40 cm high. A slot in the front wall of the box, through which an animal could reach to grasp the pasta, was 5 cm from the side of the box, 30 cm high and 2 cm wide. On the outside of the box, in front of the slot, there was a shelf mounted 4 cm above the floor, measuring 3.5 cm wide and 10 cm long. On top of the shelf (centered in front of the slot) was an open-ended frame measuring 5

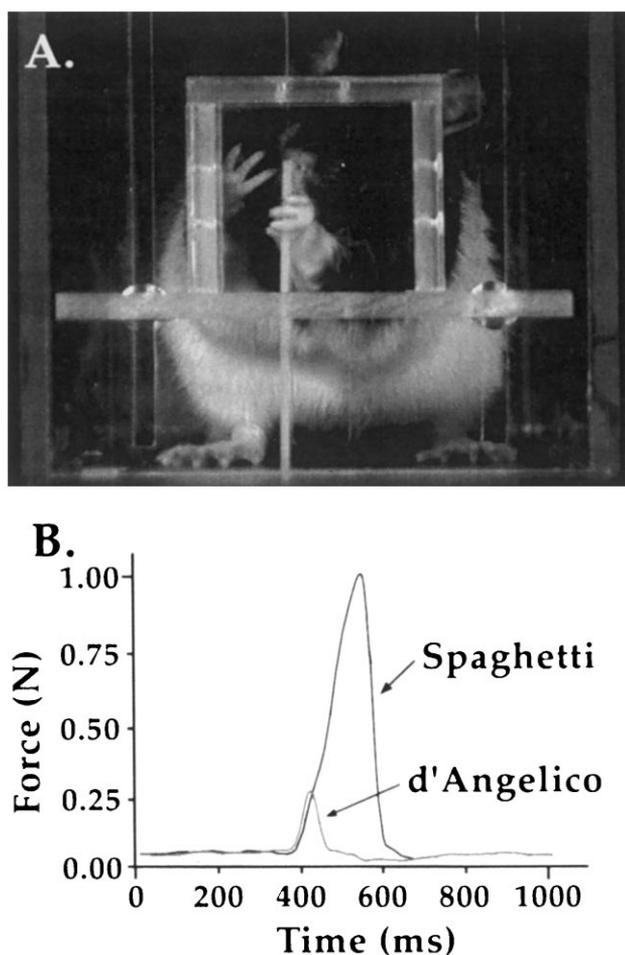


Fig. 1. A: Rat reaching in the pasta-reaching task. The non-preferred paw is frequently used to brace the rat while it applies force to the pasta. B: The rat applies different amounts of force to break pasta of differing thicknesses. Thicker spaghetti has a much higher threshold to break than thinner pasta d'angelico.

cm high by 5 cm wide by 3 cm deep. Two holes (diameter = 2.3 mm) were located on each wall, the floor, and the roof of the frame for the insertion of pieces of pasta. The holes located on the floor (the shelf) and roof of the frame were aligned with the edges of the slot. The holes in the wall of the frame were 1.5 and 3.0 cm above the floor. All the holes were 2 cm away from the front of the box. Pieces of the pasta or other target objects were placed into the holes so that they protruded a distance of 25 mm into the center of the frame.

2.3. Force measurements

The force applied to the pasta was measured by attaching the pasta to a force transducer (Aurora Supra sensor, Bokam Engineering, Santa Ana, CA) using a metal collar. The collar was held securely to the post of the transducer and the pasta using two separate thumb-screws. The voltage output was captured to a PC computer using Windaq acquisition software (DataQ Instruments, Akron, OH). The transducer was calibrated using known weights hung from the pasta at a distance of 25 mm. The output of the transducer under a known weight allowed the calculation of a conversion factor from Volts to Newtons.

Profiles of the force applied over time were acquired by removing the shelf of the apparatus described above, and using a bench clamp to place the collar of the transducer in the same location as the shelf of the apparatus holding the pasta. The pasta length was kept constant at 25 mm. The acquisition software was set to sample at 60 cycles per second. Examples of force curves were then exported into spreadsheet software for graphing (Fig. 1B).

2.4. Food and target objects

The two different food items used were uncooked spaghetti (1.6 mm diameter), and uncooked pasta d'angelico (1.0 mm diameter). Non-food items consisted of a 2.5-cm long metal rod (1.6 mm diameter), the same thickness as the spaghetti, and a serrated portion of a drill bit (1.6 mm diameter).

2.5. Videorecording under room and infrared light

The animals were filmed using a high-speed camera to film at 60 frames/s (Peak Performance Technologies, Englewood, CO). Filming was done under a Nikon cold light source at a shutter speed of 1/2000 of a second. They were also filmed in complete darkness, using an infrared camera (Sony CCD-TRV615) and external infrared light source (Sony HVL-IRH).

2.6. Kinematics analysis

Cartesian characteristics of reaching movements as well as the movement of the pasta when it was grasped and broken free from its anchor were analyzed by digitizing body parts on successive video fields using Peak Performance Motion analysis equipment (Peak Performance Technologies, Englewood, CO).

3. Procedure

3.1. Limb adjustments to changes in pasta orientation

The animals were trained for 15 sessions after which they were given food ad libitum. During the training sessions, the animals were allowed to reach with either limb, but once they displayed a preference, the pasta was placed in the hole contralateral to their preferred limb. During these training sessions, the pasta was rotated through the four positions (it was located in the lower holes of the walls and contralateral to the preferred paw in the floor and roof). The pasta was placed in these holes to allow the animals to reach it with an elbows-in posture. In order to obtain the pasta, the rat had to adjust its paw orientation and grip for each position. All rats continued to use their preferred paw for the remainder of the study.

Once the rats had completed the training sessions, they were tested in one of two sequences. In the moving sequence, they were given 20 trials where the pasta changed position after every trial. In the constant sequence, the pasta was presented for five trials in one position, then it was moved through the four positions until the animals had performed 20 trials. Using frame-by-frame analysis of the video record, all limb and paw movements used to obtain the pasta were counted. The movements were subdivided into the following categories:

1. Attempts. An attempt was defined as a forward motion of the forepaw that carried the forepaw through the aperture but which did not result in contact with the pasta.
2. Touch. A touch was defined as a forward motion of the forepaw that resulted in contact with the pasta.
3. Grasp. A grasp was defined as contact with the pasta during which some or all of the rat's digits closed around the pasta.

3.2. Kinematics analysis

Two features of grasping behavior were digitized for kinematic analysis, the position of the rat as measured by nose and paw location just prior to a grasp and the movement of the pasta as it was grasped and broken free of its anchor. The spatial model included two

reference points (the bottom left and bottom right points of the Plexiglas frame), the nose, the second and fifth digits, and the tip and base of the pasta.

1. Nose and paw position. Nose and paw location just prior to contact with the pasta was measured from two rats. Five reaches were recorded for each pasta position for each animal and these measures were made in both the light and infrared conditions.
2. Movement of the pasta. The same data set was used to measure the movement of the pasta as it was broken. The tip and the base of the pasta was digitized over a series of frames including the grasp, the movement required to break the pasta, and after the pasta was snapped from its anchor.

3.3. Tactile discrimination

For the tactile discrimination task, four animals were presented with two horizontal stimuli, placed in the two holes in the vertical wall of the frame contralateral to the preferred paw. One was a 2.5-cm long (1.5 mm diameter) drill bit attached to a short piece of pasta by a nylon cable tie, which coupled the distal end of each object. The other stimulus was a normal piece of pasta. Thus, the same torsion force would break off each item, and so the rats were required to discriminate between the objects. The animals were given 50 trials per day for 8 days. The location of the food and non-food item alternated after every trial. Correct responses and errors were scored:

1. Correct trial. A correct trial was scored when an animal grasped the metal stimulus, but did not apply sufficient force to break it, and subsequently chose and broke the pasta.
2. Error. An error was scored when the rat broke off the metal stimulus.

If the animal committed an error, they were given a 30-s delay before the next trial began. The percentage of correct responses was determined by dividing the number of correct trials by the number of correct plus error trials multiplied by 100%.

On the 9th day, the day following discrimination training, the drill bit was replaced with a 2.5-cm long (1.5 mm diameter) smooth metal rod and the rats were given 50 probe trials, the assumption being that the smooth metal rod would not be sufficiently distinct from the pasta to be discriminated.

3.4. Force measures of discrimination performance

In order to verify that the rats could discriminate the serrated metal rod from the pasta, some sample force measures were taken during contact with the smooth metal rod and the serrated metal rod.

4. Results

4.1. Movements used for grasping pasta

The initial movements in reaching for pasta are identical to those seen in other reaching tasks [34]. The rats lifted their preferred limb, and closed their digits all while bringing the paw to the midline. From this position they then aimed their paw at the food item and advanced their paw toward it. During the advance phase of the reach, the digits opened to make contact with the food. From the digits open position, the rats made contact with the pasta and either closed their digits around it, or withdrew the forepaw to the aperture to begin another attempt. Once a rat closed its paw around the pasta, it applied force medially and in the posterior and ventral directions simultaneously. If the force was insufficient to break the pasta, the rat released the pasta to withdraw its paw to make another attempt. Once the pasta had been broken, a rat made rotatory movements of the forelimb to withdraw the pasta through the slot. Depending on the orientation of the pasta, the rotatory movements could involve either pronation or supination. Finally, the rat transferred the pasta to both paws and manipulated it to consume it. The examination of these movements under room and under infrared light indicated no detectable difference in movements used in orienting, grasping, or retrieving the pasta (Total Movements: $F_{1,6} = 0.349$, $P > 0.05$).

4.2. Body and limb adjustments to changes in pasta orientation

To obtain pasta oriented in different directions, the rats were required to adjust their paw location to achieve a successful grasp and break to obtain the pasta. Typical paw orientations after the paw contacted the pasta but just before the digits closed on the pasta are shown in Fig. 2.

To determine whether the limb adjustments were predetermined or were tactile adjustments to the pasta, both body orientation and paw adjustments were measured. Body orientation was determined by measuring the location of the nose of the rat and the location of the second digit of the reaching forepaw during limb advancement (before contact with the pasta). The measures of nose and forepaw locations were the same for pasta in the four different orientations (Fig. 3). Two-way ANOVAs performed on both the nose and the forepaw in the X and Y directions gave no significant differences ($F'_{3,6} < 1.80$, $P's > 0.05$).

In contrasts to the stereotyped posture and limb advancement, there were many paw adjustments following the initial paw advance. The animals made a number of limb advances and withdrawals in order to locate the pasta, and they then made further adjust-

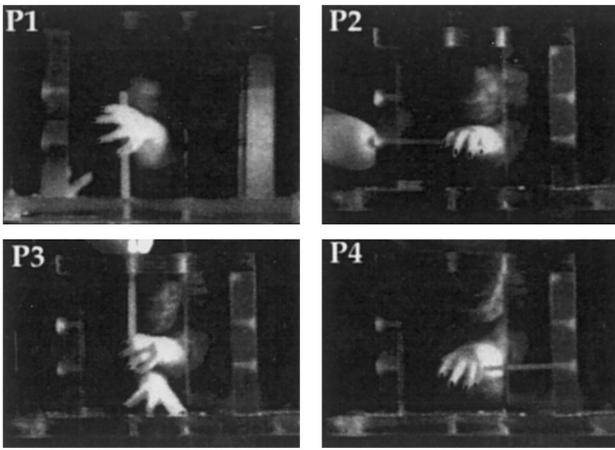


Fig. 2. Four different reaching positions for a rat using its left paw. For each orientation, the frame is that occurring after contact, and preceding digit closure. For all four orientations, the rats rely on tactile information to orient their paw to the pasta. Note: the paw orientation is obviously different for different pasta orientations.

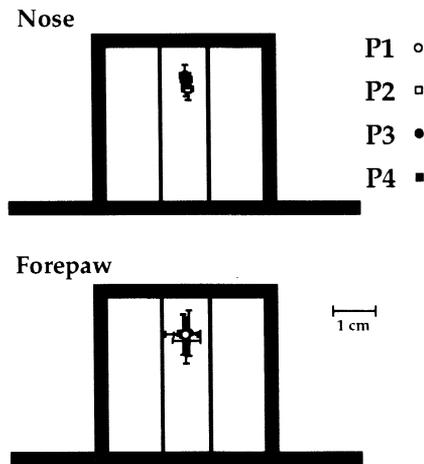


Fig. 3. The position (mean and S.D.) of the rat's nose (top) and forepaw (bottom) during the initial reach for four pasta orientations (P1–P4). The constancy of these positions shows that the posture does not change to accommodate the changing location of the pasta.

ments to grasp the pasta, and finally once they had grasped the pasta they frequently moved their paw to obtain an optimal location from which to break the pasta from its anchor. The animals made more grasp movements regardless of the orientation of the pasta (t -tests, df 7, $t = -3.372$, $P < 0.01$; Fig. 4). The number of paw adjustments was very similar for each pasta orientation (Total Movements: $F_{3,24} = 2.611$, $P > 0.05$) and for each training sequence ($F_{1,8} = 0.006$, $P > 0.05$; Fig. 5).

A number of grasp patterns were used in obtaining the pasta, depending upon the orientation of the pasta. Grasp patterns included grasping the pasta with digits 2 through 5 in a 'whole paw' grasp, grasping with digits 3 and 4 in a 'hook' grasp, or more commonly grasping

with a 'scissor grasp' by placing digits 2 through 4 over the dorsal surface of the pasta and digit 5 underneath the pasta. Once the rats acquired the task, they used the scissor grasp in about 80% of all trials.

4.3. Pasta break

The direction of the pasta movement as it was broken from the anchor was recorded and analyzed using Cartesian measures of the movement of the pasta just prior to and following breaking. For each pasta orientation, the pasta was broken in a direction that suggests the animals are applying a force that is medial and caudal in direction to the preferred paw (Fig. 6). Stated differently, the forces applied to the pasta were similar to forces applied in human arm wrestling, medially and caudally. Thus, for the various orientations, the paw and limb movement required to break the pasta was slightly different.

4.4. Tactile discrimination

The animals were trained to discriminate between the serrated drill bit stimulus, and the pasta (Fig. 7), then were tested to find their baseline performance on a smooth stimulus. Over test sessions there was a declining incidence in which the rats broke the rough discriminanda from its anchor, showing that they were able to discriminate the serrated drill bit from the pasta. That is, by day 6, the rats released the rough stimulus on close to 80% of trials on which they contacted it with their paw.

When a smooth stimulus replaced the rough stimulus, performance significantly dropped to $\sim 40\%$ ($F_{1,2} = 31.796$, $P = 0.03$; Fig. 8). When force measures were used to compare grasps exerted on the rough

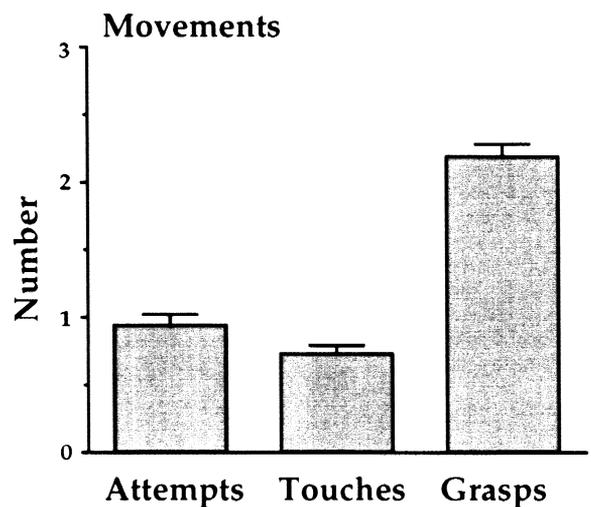


Fig. 4. The number (mean and S.E.) of each type of movement during reaching for pasta collapsed over all four pasta orientations.

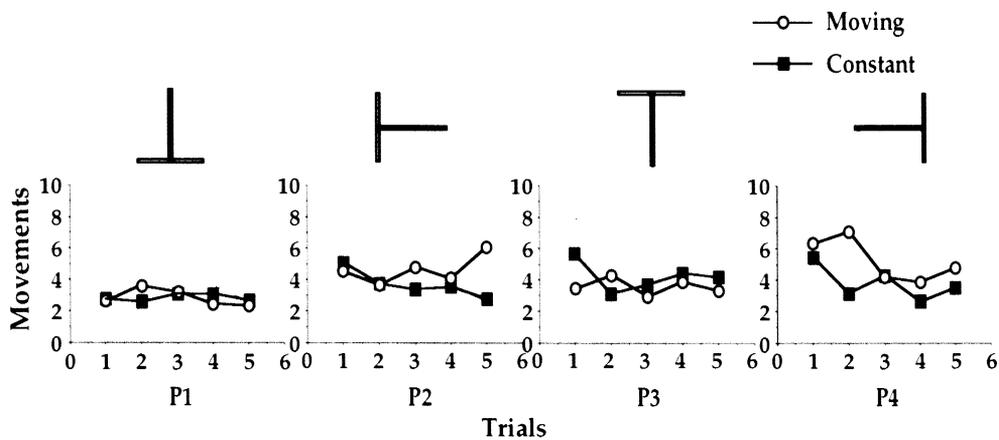


Fig. 5. The mean number of grasp movements performed in the four different pasta orientations, in the constant (five successive trials in one position) and moving (one trial in each position) presentation sequences. Note: rats make the same number of grasping movements regardless of the orientation of the pasta and whether the orientation of the pasta changes after every trial or not.

versus the smooth stimuli, it was readily apparent that the rats released the rough stimulus after contacting it rather than breaking it free from its anchor as they did with the smooth stimulus (Fig. 9).

5. Discussion

The purpose of the experiments was to examine whether rats can use tactile information during a skilled reaching movement to modify features of that movement. It was found that when rats reached for pasta held in different orientations, they used a common posture and reaching strategy irrespective of the orientation of the target. Nevertheless, in order to successfully grasp a piece of pasta and break it free from its anchor, they did modify their reach trajectory, grasp pattern, and paw movements. Discrimination and force measures of grasping indicated that they were also able to discriminate between different stimulus items. These results show that the rat can modify its grasping movements using haptic information, thus indicating that the sensory processing used in prehension by the rat is similar to that of carnivores and primates.

5.1. The rat's reaching strategy

Previous studies on rats reaching for food pellets on a shelf show that they first identify the location of a food item using olfaction and not vision [28]. That is, rats that were anosmic reached 'as if blind' and only obtained food by chance, whereas rats wearing blindfolds were indistinguishable from control rats in accuracy of locating and reaching for food items. Once they have located food, the rats advance a forelimb by lifting the paw while at the same time bringing the digits to the midline of the body with the palm facing medially.

They then adduct the elbow so that the paw is in an aiming position, oriented in parallel with the midline of the body. From this position, the forelimb is advanced while at the same time the nose is lifted away from the target item to allow the forelimb access to the food item [26,27]. As the forelimb is advanced, the digits are opened, the paw is pronated by adduction of the elbow and rotation of the wrist, and the digits are flexed and placed around the target in an arpeggio movement [25].

Examination of the reaching movements used by the rats in the present study indicated that movements of

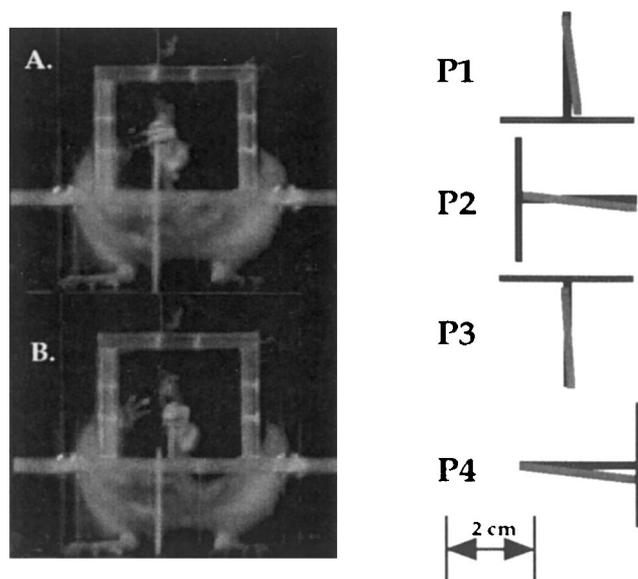
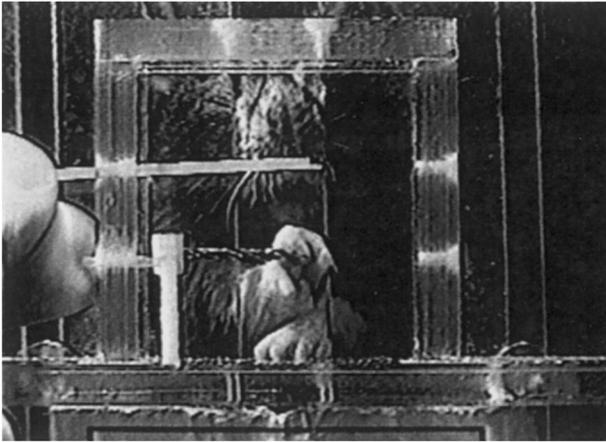


Fig. 6. The solid line in the cartoons indicates the pasta and its orientation. Shown is the direction of the break from one frame before the snap (A), to the frame where the snap actually occurred (B), for four pasta orientations (P1–P4). Note: For the four positions the direction of the pasta movement implies that the force applied is medial and caudal. The mean deflection in the X and Y directions for both the tip and the base is presented here.

A. Discrimination Task - Rough



B. Smooth



Fig. 7. Tactile discrimination task. A: Training trials were done with the rough metal stimulus bound to a piece of spaghetti. B: Probe trials were done with the smooth metal stimulus.

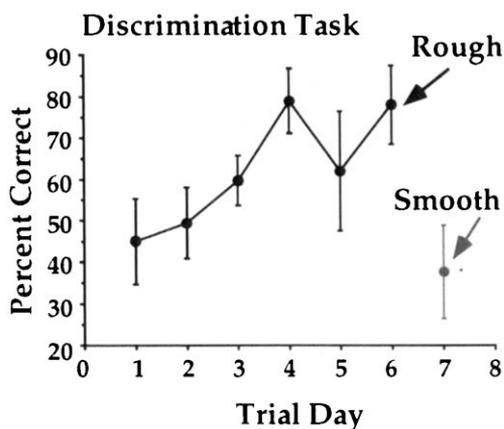


Fig. 8. Percentage (mean and S.E.) of correct discriminations on training stimuli (rough) and probe stimuli (smooth). Note: over training sessions, the rats learned to inhibit breaking the serrated (rough) discriminanda from its anchor.

reaching for pasta are very similar to the movement used in reaching for food pellets. The similarities in-

cluded orienting to the food by sniffing, lifting and aiming the forelimb, and advancing the forelimb as the head is raised. Even when the pasta was in different orientations, the final positions of the nose and forepaw during limb advancement were similar. Together these observations indicate that the rat is unable to detect the orientation of the target using olfaction and thus is constrained to using a common posture and limb advancement for all orientations. This conclusion was further confirmed by testing the rats in infrared light, a portion of the spectrum in which rats are unable to see [22]. In this condition, their reaching posture and movements were identical to that observed in room light conditions, confirming that they are also unable to use vision, but did use olfaction, to appropriately orient and direct their reaches to the different targets.

5.2. Modifications of the grasping pattern

Despite the stereotyped postural adjustments used by the rats in initiating a reach, they did make adjustments in their reaching trajectory, grasp pattern, and direction of force application in order to obtain differently oriented pieces of pasta. Typically, they made one to two preliminary limb advancements through the aperture leading to the pasta. These movements did not always contact the pasta and so were likely used to confirm the location of the aperture and the frame holding the pasta. Likely these orientation movements gathered information not only via paw and digit contact with different portions of the apparatus but also by stimulation of the sinus hairs located on the ulnar surface of the animal's wrist. Following these preliminary reaching movements, the animals made further reaches in which they contacted the pasta with different portions of the paw. These contacts rapidly led to paw adjustments in which the pasta was grasped.

A number of grasp patterns were used in obtaining the pasta, depending upon the orientation of the pasta.

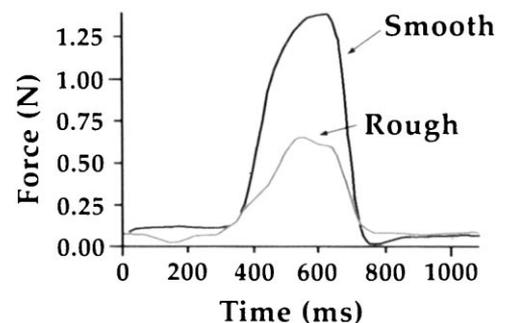


Fig. 9. Force applied to the serrated metal rod (rough) and smooth metal rod after the tactile discrimination task was learned. The rats do not exceed the threshold to break the spaghetti when the rough stimulus is used, but do apply sufficient force to break off the smooth stimuli.

Grasp patterns included grasping the pasta with digits 2 through 5 in a ‘whole paw’ grasp, grasping with digits 3 and 4 in a ‘hook’ grasp, or more commonly grasping with a ‘scissor grasp’ by placing digits 2 through 4 over the dorsal surface of the pasta and digit 5 underneath the pasta. These various grasp patterns are also used by rats in spontaneously holding food objects of various shapes and sizes during eating [24]. Finally, rats were also able to adjust their paw position once they had grasped the pasta. These movements typically consisted of opening the paw after it had made an initial grasp and moving it to a better position on the pasta. Since the optimal position for breaking the pasta was toward its distal end, these movements consisted of a variety of horizontal or vertical adjustments, depending upon the pasta’s orientation, in order to obtain appropriate purchase. It is likely that tactile information gathered from sensory receptors on the paw is involved in all of these limb and paw adjustments.

Rats also appeared to use tactile information in order to apply appropriate torsion to variously oriented pieces of pasta. Kinematic measures of the movement of the pasta as it was snapped from its anchor indicated the direction of the paw movement and of the force applied to the pasta changed with orientation, indicating that the rats were adjusting the direction of their pull as a function of the pasta’s orientation. Thus, it is likely that tactile information is used to determine the direction of pull. When rats grasp a food pellet from a shelf, the closure of the digits around the food pellet is typically followed by flexion of the wrist in order to lift the food from the shelf [25]. It is thus likely that after a rat grasps the pasta, it modifies the direction of wrist flexion in order to apply appropriate torsion. In future studies, we will develop force sensors that will detect the breaking forces applied in various directions. Such measures should confirm that breaking forces are adjusted as a function of pasta orientation.

5.3. The use of hapsis in target discrimination

In order to confirm that the rats used haptic information for grasping and breaking the pasta, the animals were given a discrimination test. A piece of pasta and a similar size serrated metal rod, attached to a piece of pasta, were used as discriminanda and their location was alternated between two horizontal locations. Thus, an animal was required to learn that if its paw contacted the metal bar and broke it free from its anchor it would not receive reinforcement. Over a series of training sessions, the animals learned not to pull on the serrated metal bar when their paw contacted it. That they made a tactile discrimination was confirmed by substituting a smooth metal rod, that had the size and texture of a piece of pasta, and also by comparing the force that they applied when grasping pasta, the ser-

rated metal rod, or the smooth metal rod. The results of these measures indicated that when the rats grasped pasta or the smooth metal rod they immediately applied traction and broke the objects free whereas if they grasped the serrated metal rod, they applied little force and then released it. Because the animals could not discriminate between the smooth metal and the pasta, this information indicates that the animals did not use thermal differences (i.e. heat conductance) between the discriminanda to make their discriminations. Thus, taken together, these tests indicated that after grasping a target object the animals could use haptic information to make a decision about whether to pull it free.

5.4. Implications and conclusions

In contrast to carnivores such as the raccoon [11] and primates [16], hapsis has not been thought to play an obviously central role in rat reaching performance in laboratory reaching-for-food tasks. In contrast, there is considerable evidence that rats make extensive use of hapsis in spontaneous food handling, during which they sit on their haunches and manipulate food with their digits [24]. Nevertheless, the central finding of the present study is that rats can, and do, use haptic information in a variety of ways to adjust their reach trajectory, grasp patterns, and lifting strategies during skilled reaching. Indeed, many of the inaccurate grasps typically recorded in skilled reaching tasks may be haptic limb excursions [29]. This conclusion is consonant with anatomical evidence that rat tactile receptors and somatosensory pathways are similar to those of other mammals [14,23]. That rats use haptic information when reaching should be useful in devising experimental procedures to study sensory control of skilled movements in rodent experimental models of disease of sensorimotor systems [17].

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