

Kinematic Strategies and Sensorimotor Transformations in the Wiping Movements of Frogs

SIMON F. GISZTER, JOSEPH McINTYRE, AND EMILIO BIZZI

Department of Brain and Cognitive Science, Massachusetts Institute of Technology, Cambridge, Massachusetts 02139

SUMMARY AND CONCLUSIONS

1. Spinal frogs are known to make coordinated and successful wiping movements to almost all places on the body and legs. Such wiping movements involve a sensorimotor transformation. Information from both the spatial locations of stimuli on the skin and the body configuration of the frog is transformed into a set of motor commands that generate body movements adequate to successfully remove the irritant. The spinal cord itself therefore has a limited capacity for sensorimotor transformations.

2. We examined the kinematics of wiping motions in both spinal and intact leopard frogs and bullfrogs. This data was used to assess the flexibility, precision, and strategy of the kinematic sensorimotor transformations used during wiping. The movements involved the use of redundant degrees of freedom in the limbs. Thus many possible movements or solutions could generate successful wiping. This redundancy allows motor-equivalent movements to be used by the frog.

3. Movements were examined in two dimensions by the use of VHS shuttered-video recording and in three dimensions with the use of a WATSMART system of infrared diodes and cameras. The kinematic analysis was applied to those motions in which the limbs did not interact with kinematic constraints, such as the surface of the substrate or body. These unconstrained motions are directly related to motor commands and thus more easily interpreted.

4. Wiping movements to the back were retained in essentially the same form in both spinal and intact frogs. In both cases wiping had four phases with a fifth occasionally present. The phases included flexion, placing, aiming, and whisking, with occasional extension and multiply repeated wipes. However, the aiming phase was often very brief or absent in this data, and flexion was sometimes omitted in multiple wipes. We found that the placing posture was adjusted in a simple way in response to variations in the location of the target stimulus. The rostrocaudal position of the foot tip was strongly and linearly related to the rostrocaudal stimulus location.

5. During the placing posture, joint angles as well as the limb tip in back wipes had linear relationships to the stimulus' rostrocaudal coordinate. The limb configuration used by the frog allowed a strategy of linear (and potentially independent) postural adjustment of joint angle to stimulus position to generate almost linear endpoint adjustments in the placing phase of wiping. This solution to the ill-posed problem of choosing a joint angle for the placing posture in back-wiping may be computationally simple. The solution allows a parallel and independent determination of desired joint angles to be performed. The transformations needed for back-wiping may be considerably simplified by this strategy.

6. In hindlimb-to-hindlimb wiping, the movements of intact and spinal frogs differed. The hindlimb wipes of spinal animals showed a reduced workspace coverage as compared with the hindlimb wipes of intact animals. In intact frogs, the configuration and location of both the target and the effector limb varied widely. By contrast, the same animal was extremely stereotyped

following spinal transection. Using configuration information, intact frogs appeared able to perform both the inverse and forward kinematics transformations necessary for planning flexible adjustments in this wiping task. In contrast, movements of spinal frogs were precise and stereotyped in multiple wipes to the same stimulus location. This evidence suggested that a fixed kinematic plan or strategy was simply triggered in the spinal animals.

7. We hypothesized that the hindlimb wiping used by the isolated spinal column involved a fixed strategy and was not finely adjusted in response to configuration information. Stimulated target limbs were held fixed in different postures or were perturbed as wiping began. When the target limb was immobilized at a long distance from the normal zone of spinal wiping, the animal's wipes to the stimulus began to miss. At further distances the frog began to perform motions that were different from normal wiping. These new movement patterns sometimes took the limb away from the target rather than towards it. When a moving target limb was perturbed away from the normal wiping zone, two types of results occurred: missed wiping or premature termination.

8. The spinal frog is able to make simple sensorimotor transformations and perform adjustments based on cutaneous stimuli. Cutaneous sensory information is incorporated in a smooth, continuous, and nearly linear fashion into the sensorimotor transformations. Small variations in stimulus location lead to small adjustments in motor output in both intact and spinal frogs. Kinematic redundancy may be used in the frog to simplify the computation of the sensorimotor transformations in both intact and spinal frogs. The solution constrains the degrees of freedom of the limb to allow an almost linear transformation to be used. There is little configuration-based adjustment of movements in spinal frogs. The use of proprioceptive information regarding limb configuration may be limited to discrete switching or gating functions in spinal frogs. For unconstrained movements, the patterns appear fixed for a given stimulus location on the skin in spinal animals. For stimuli in the transition zones, the patterns may vary.

INTRODUCTION

The wiping movements of frogs are coordinated, multi-joint limb movements that remove irritating stimuli from the skin. It is known that the spinalized frog is able to make coordinated and successful wiping movements to almost all places on the body and legs. (See Fukson et al. 1980; Sherrington 1906; and the historical review by Reed 1986.) Wiping, scratching, grooming, and paw-shaking responses in several animals have been used as model systems for examining multi-joint limb movements (Fukson et al. 1980; Golani and Fentress 1986; Mortin et al. 1985; Robertson et al. 1985; Smith et al. 1986; Stein 1983).

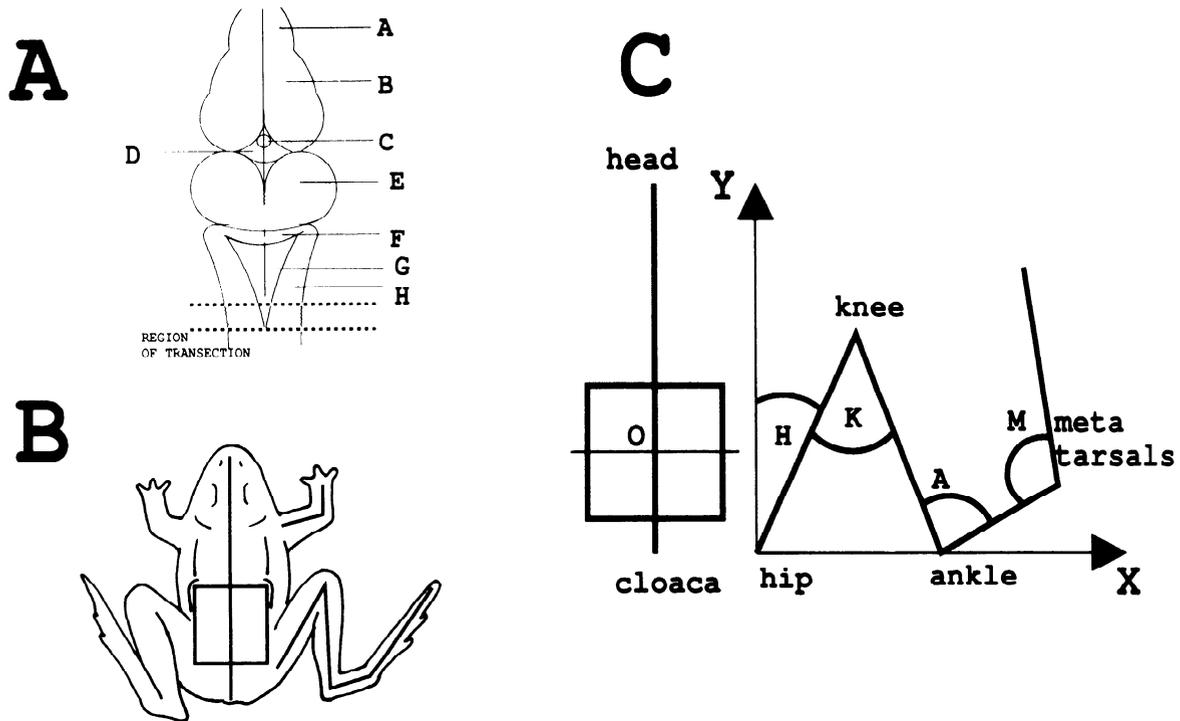


FIG. 1. *A*: principal features of the frog CNS that were exposed and ablated during surgery are shown in this panel of the figure. These are A, Olfactory lobes; B, cerebral hemispheres; C, pineal gland; D, thalamus; E, optic lobes; F, cerebellum; G, fourth ventricle; and H, medulla. Because of variations of aspiration and positioning of the head, the transection site was known to be within a band of ~ 2.5 mm extent. *B*: schematic of the video image of a frog and the points measured on this image in the captured frames. These points are indicated by a box over the anterior protrusion of the pelvis, the snout, cloaca, and estimated hip joint, knee joint, ankle joint, and astragalus-calcaneum to metatarsal joint. If forearm locations were being stimulated, shoulder, elbow, and wrist joints' positions were also digitized. The Cartesian coordinate system we used was centered on the centroid of the pelvis box. This allowed the angles displayed in *C* to be constructed. *C*: joint angles measured in the images. X-Y coordinate axis was centered at the origin at O. Hip angle (H) was measured relative to the Y axis. Other angles were measured relatively [Knee (K), ankle (A), and metatarsal angle (M)]. Internal angles were positive by convention. Angles measured were extension or flexion of each joint.

Successful wiping requires the execution of a movement that is adequate to remove an irritating stimulus. The movement must take into account the location of the stimulus on the skin and the configuration of the body during the execution of the wipe. Thus the frog performs a transformation of sensory information into a coordinated motor output.

Some degree of adjustment of motor output must occur based on the sensory configuration. This adjustment could simply be the choice of one of a few discrete movements, or it could be a complex and continuously varied adjustment of movements.

The frog's hindlimb has redundant degrees of freedom in positioning the foot during the wiping task. The frog must therefore solve Bernstein's problem (1967) of choosing one movement plan from among many possible motor-equivalent solutions. In robotics, redundant degrees of freedom can be utilized to satisfy additional constraints on the system. Proposed control schemes include use of the redundancy to minimize joint velocities (Whitney 1972), avoid obstacles and joint limits (Hildreth and Hollerbach 1985), and minimize change in potential energy of the limb (Mussa-Ivaldi et al. 1988). Exactly how the spinal frog may be exploiting the redundancy is not yet clear.

In this paper, we have examined the following questions: 1) How is sensory information about target location transformed into an appropriate limb configuration in the unconstrained placing posture during the wiping movements of a frog? 2) By what mechanism does the frog resolve kinematic redundancies in order to produce a single solution for a particular trial? 3) Is the limb truly redundant in all postures, or do joint limits reduce the degrees of freedom in some areas of interest? 4) To what degree, if any, can the frog modify its choice of motor commands? Specifically, does the frog execute a fixed strategy for a given target location, or can the movement vary from trial to trial? 5) Are variations in movements continuous or discrete? and 6) How does the performance of the spinal frog differ from that of the intact frog?

To address these questions, we have made a careful examination of the kinematics of wiping movements in both intact and spinal frogs. A particular kinematic pattern is the final result of all the transformations from stimulus location and body configuration into muscle commands. An examination of kinematics in well-defined frameworks has often been used to obtain insight into motor control (Abend et al. 1982; Atkeson and Hollerbach 1985; Flash and Hogan 1985; Lacquaniti and Soechting 1982; Morasso and Mussa-Ivaldi 1982).

MATERIALS AND METHODS

Large adult leopard frogs (body length 8–10 cm) and bullfrogs (body length 15–20 cm) were used in this study. Animals were maintained in a vivarium at 20°C until used in experiments.

We examined wiping movements in intact and freely moving animals, as well as in spinalized animals in both free and restrained conditions.

Surgical procedures

LEOPARD FROGS (*RANA PIPIENS*). Twenty to 40 min after anesthetizing leopard frogs with an intramuscular injection of ketamine hydrochloride (0.02 ml, 100 mg/ml), we surgically exposed the area of the foramen magnum and skull. The head was flexed ventrally across a steel bar, and the muscles of the neck were carefully retracted along the dorsal midline. The skull was opened using a high-speed drill (Bermann Osteotome) and the opening widened with bone rongeurs to expose the brain and cervical spinal cord. The brain anterior to the calamus scriptorius was then aspirated away using a micropipette attached to a Sklar aspirator operated at full-power aspiration (See Fig. 1A and Ecker 1971; Kemali and Braitenburg 1969). The resulting cavity was filled with Gelfoam soaked in frog Ringer (Richards 1936).

BULLFROGS (*RANA CATESBEIANA*). Bullfrogs were anesthetized with injections of 1 ml of a 5% solution of Tricaine (MS-222 Sigma) into the dorsal lymph sacs. This solution was chosen since we found that ketamine anesthesia frequently killed bullfrogs. The muscles of the neck were separated and retracted to expose the foramen magnum, and the head was flexed ventrally across a steel rod. We did not aspirate and remove the rostral central nervous system in the bullfrogs because they never survived aspiration of large portions of the nervous system in our hands. Instead we used fine scissors to expose and transect the brain stem at the level of the calamus scriptorius. The two pieces were physically separated. The anterior nervous system was pushed forward slightly to ensure a full transection. The gap was gently filled with Gelfoam soaked in frog Ringer.

Both leopard frogs and bullfrogs were maintained in the same way following transection. The animal was placed on a moist pad contained in an unsealed closed plastic case in a refrigerator at 8°C. Animals were allowed to recover for 1–5 days before we recorded movements. The best recovery of activity occurred at 4 days and beyond, although with repeated sessions of stimulation an animal's performance often declined. In some cases, spinalized animals could be maintained alive in this cooled state for periods of up to 3 wk while being repeatedly examined at a room temperature of 20°C.

Stimulation of wiping

We elicited and examined wipes in both intact and spinal frogs. Wiping movements could be elicited in several ways. In intact animals, we used a punctate stimulus consisting of a 20-g, 1.5-in hypodermic needle mounted on a long rod. Stronger stimuli were needed in the spinal animals. A vibrating punctate stimulus or the electrical stimulation of a skin patch sometimes gave rise to wipes in trials before the experiment. However, the most consistent stimuli for generating all wiping movements were small (1 or 2 mm) squares of Fiberglas filter paper soaked in 0.5 M sulfuric acid. We used these filter-paper acid stimuli in the spinal frog recordings described here.

Movement recording

Three types of wipes were recorded from the frogs' repertoire. These were 1) wipes to the back, 2) wipes to the forelimb by the use of the ipsilateral hindlimb, and 3) wipes utilizing one hindlimb to wipe the contralateral hindlimb. The back and hindlimb

wipes were readily elicited and could be obtained in both intact and spinal frogs. We were unable to elicit forelimb wipes routinely in intact frogs. Other responses, such as forelimb withdrawal and oriented snapping, also occurred. Recording methods differed for the different types of wipes. It was possible to use the fast three-dimensional WATSMART recording system on the hindlimb-hindlimb wiping of spinal bullfrogs. However, for the hindlimb-hindlimb movements of intact frogs, this approach was not feasible because infrared-emitting diode markers (IREDS) could not be attached to these animals. IREDS could not be attached without interfering with the movements of intact and spinal frogs as they wiped to the back. VHS video-recording techniques were used in these cases.

VIDEO RECORDING. It has been reported that wipes to the back involve very little motion of the effector hindlimb out of a plane (Berkinblitt et al. 1984). This observation was confirmed here using 30-Hz video recordings of the movements with a mirror angled in the field of view to allow all dimensions of the movement to be viewed. Subsequently, measurements of limb configuration and position from the video were made, choosing a planar representation of this wiping. The loss of information about actual angles was small. Two degrees of freedom at the hip were not captured, and a measure of distortion of the limb's remaining joint-angle estimations was introduced. The degrees of freedom lost, namely elevation and rotation at the hip, acted primarily to bring the plane of motion of the other joints parallel to the back surface and into the plane viewed in the video.

Selected frames were digitized using a frame-grabber operated from a Symbolics LISP machine and a combined composite/RGB monitor with a Panasonic VHS editing deck. This set-up allowed rapid switching between color composite and digitized images to examine the quality of the image captured. A computer-generated graphic of a box was scaled to the size of the frog in the videotaped image. This image was adjusted so as to span the pelvis from the anterior and lateral protrusion of the iliac bones to the estimated center of the acetabulum. Using a mouse-type positioning device, we oriented the box over the protrusions of the rostral pelvis on the image. The tip of the snout, the hip, knee, ankle, and metatarsal joints, and the tip of the foot were digitized. We also recorded the location of the target stimulus on the body scheme. If the target was on the forelimb, we digitized the shoulder, elbow, and wrist of the target limb.

Errors in digitization originated from two sources: first, problems with the pointer device and video resolution, and second, difficulty of estimating joint centers. Digitization errors in measuring positions from the VHS images were large enough to make incorporation of the small variations in the mirrored perpendicular view unfeasible. Problems in the planar projection were a less significant source of error than digitization errors within the plane. These latter errors derived from difficulty in estimating joint centers of rotation. Errors in digitizing position for clearly marked points amounted to <5 pixels in a screen of 576 (horizontal) × 454 (vertical) pixels. Figure 1, B and C, shows the measured features of an image and the coordinate systems used. See below.

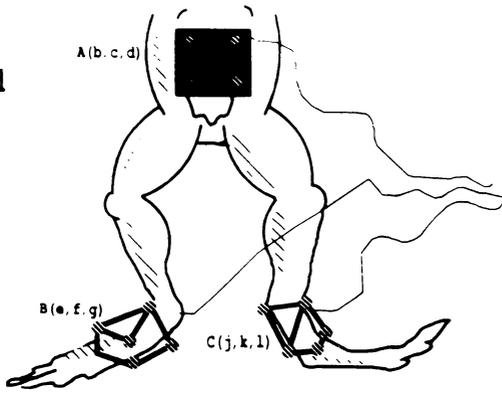
Errors because of deviations in the digitized joint location about actual joint location were estimated from repeated digitization of single frames. These errors could be modeled as Gaussian errors about a real joint location. This technique allowed us to estimate joint-angle errors for a particular limb configuration. These errors depended both on the position-estimation errors for the joints and on the lengths of the links on either side of a joint.

About 45 leopard frogs were examined using the video technique alone.

WATSMART TECHNIQUES. These techniques are summarized in Fig. 2. Fifteen IREDS in three arrays of 5 each were firmly attached to the pelvis and the astragalus of each leg. Cyanoacrylate glue was used to secure the attachments. Aluminum wire on

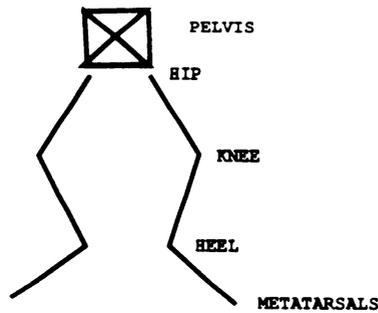
Frog Instrumented with IREDS

A



Stick Figure Reconstruction

B



Joint Angle Reconstructions

C

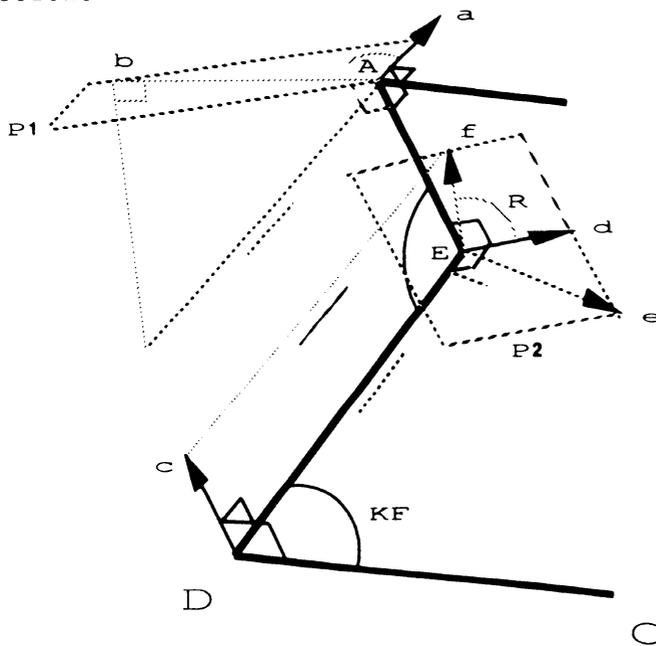


FIG. 2. Data processing stream used for WATSMART data. *A*: diagram of IRED placement on the frog. Each array has an associated centroid and orientation, which are measured by the WATSMART system. *B*: after appropriate filtering, the centroid and orientation data were used to construct joint-angle data under the assumption of coplanar link segments. These data allowed a 3-dimensional stick figure to be constructed as shown here. Cartesian coordinate system we used was centered on the centroid of the pelvis box (body-centered coordinates). *C*: conventions we used to reconstruct the joint angles. Hip was characterized by 3 angles and the other joints by 1 angle each. A vector was constructed from the hip location (E) to the centroid of the pelvis IRED array (direction vector EA). This vector was used to define a perpendicular plane p1. We took as azimuth for the leg the angle between the projection of the thighs direction vector ED onto the plane p1 (vector Ab) and the projection (Aa) in the same plane of the cross product of the 2 hip to centroid vectors. The angle between the vector EA and the thighs direction vector ED was taken to be the elevation of the leg. Rotation of the plane defined by the axes of the thigh and calf about the axis defined by the thigh was taken to be rotation, the third angle necessary to define an angular coordinate system for the hip. The plane p2 perpendicular to the thigh's direction vector ED was defined. The cross product of DE with DC (vector Dc) as projected onto p2 (vector Ef). The angle of this vector with an arbitrary fixed vector Ed was taken to be the rotation. The vector Ed was chosen when the frog was relaxed and in the flexed sitting posture.

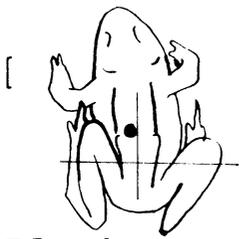
the array base was bent around the limb to hold the array firmly in place. Except in overflexion movements, the frog still had full range of motion with the arrays attached. Overflexion is not normally used in the bullfrog's hindlimb-hindlimb wiping movements, which were examined with this technique. Two WATSMART cameras were placed at 90° angles to one another. These cameras were calibrated using a small custom-made calibration

frame supplied by the Northern Digital Company. The table and all objects in the field of view of the cameras were painted with a flat black nonreflecting paint (Krylon Engine Flat Black).

During recording the IREDS were sequentially driven by the WATSMART system at a rate of 100 Hz. Using the two cameras, the WATSMART system then viewed the IREDS as they were sequentially activated. The camera information was sufficient to

1 Flexion

FRAME 1

**2 Placing**

FRAMES 5-8

**3 Aiming/whisk**

FRAME 12

**4 Whisk (a)**

FRAME 15

**5 Whisk (b)**

FRAME 20

**6 Flexion**

FRAME 25



FIG. 3. This stylized drawing of a frog wiping its back was drawn from a video of an intact animal. Stimulus location is shown by the black dot. A 1-cm scale bar and reference axes are shown for comparison with the graphs presented. The frog makes back-wipes in several stages: 1) flexion: if the frog's wiping limb is not in a flexed condition, the limb is usually initially moved into a flexed position; 2) placing: the distal joints are dorsiflexed and positioned in a precise relation to the stimulus, caudal to it; 3) aiming: the limb is moved to the stimulus, where there may be a brief pause or aiming phase. This can be incorporated into the whisk phase; 4 and 5) the limb whisks over the back, removing the stimulus; and 6) the limb returns to the flexed position.

reconstruct the IRED location in a three-dimensional world-coordinate system. Parameters derived by the calibration to the known object were used to convert 2-dimensional position data gathered by the cameras into 3-dimensional position data. Each IRED was thus located in a world-coordinate system after the data were collected (Northern Digital WATSMART System software). Each IRED array used in the experiment was first recorded under optimum conditions guaranteeing no reflections. This record was used to produce calibration data on the distances and relative vectors between IREDs in the coordinate frame of the array.

The spinal bullfrog was then instrumented with these arrays. The frog was restrained by a clip on the lower jaw and angled so that each of the cameras had a full view of all IREDs. It was important that the cameras have a full view of the IREDs throughout motion. To ensure this outcome and to minimize infrared reflection problems, we placed the frog on a plane in-

clined at an angle of 10–20° off horizontal. The frog's head was always uppermost. The positions of metatarsal joint, heel, knee, and hip in relation to the pelvis were indicated with a calibrated IRED pointer. The converted 3-dimensional data from an experiment was then filtered. The calibration parameters were used to discard IREDs whose distance from the rest of the ensemble in the array deviated by >10% of the calibration distances. In this way we removed reflections from the data. This processed reflection-free data was then further processed using the Shut algorithm (Conati 1977). This algorithm is able to extract a centroid location and orientation for each array in the world-coordinate system, provided at least three IREDs are visible and nonreflecting. The algorithm also incorporates the additional information obtained when all five are visible.

The quality of the reconstruction was tested using an arbitrary object instrumented with IREDs. This object was held in a Grass

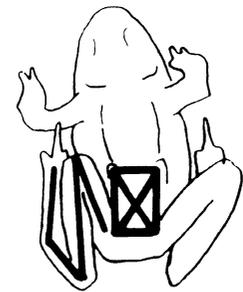
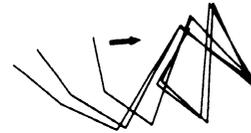
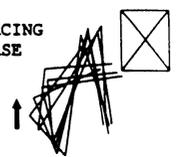
Wiping to the Back**1 FLEXION PHASE****2 PLACING PHASE****3 WHISK AND EXTENSION PHASE**

FIG. 4. A spinal frog is shown wiping to its back. This figure shows a full series of frames digitized from a video of a spinal frog wiping the back. *Top right:* digitized segments overlaid on the frog's body for comparison with the series of Fig. 3. 1) flexion: the animal draws the limb into a standard flexed position from wherever the limb lies in the workspace. Surface kinematic constraints and the joint limits act in this motion; 2) placing: the limb is elevated and rotated and the joints flexed so that the distal foot folds over the back. The only possible kinematic constraint that may operate is the metatarsal segment being constrained by the calf. This is essentially a free-space motion; and 3) whisk and extension: this is the wipe proper. The limb is lowered onto the back and moved rostrocaudally across the back to contact the target. While the limb is accelerating, and moving off the back, the stimulus is removed.

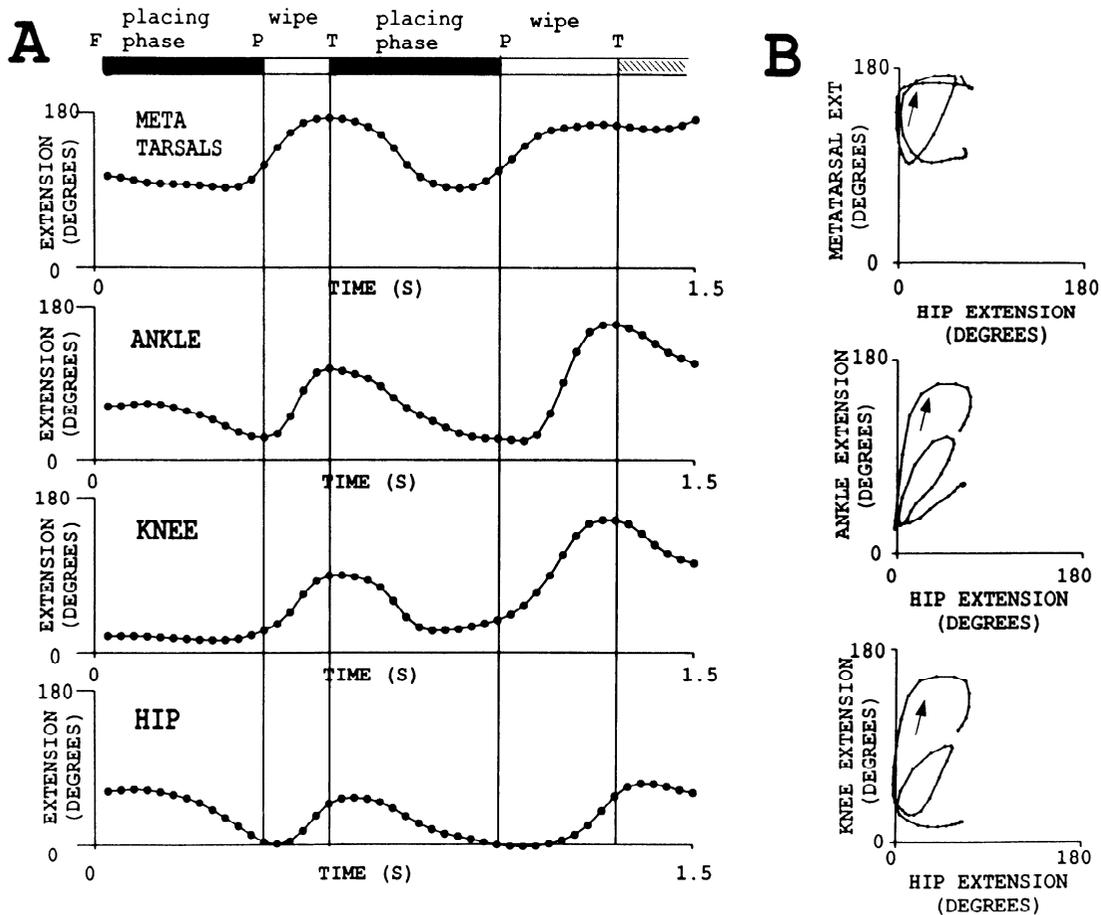


FIG. 5. Joint-angle plots for wiping to the back in a spinal frog. *A*: time series of angles during 2 wipes to the same site. Animal begins the sequence already in the flexed condition. Phases of wiping are shown. Placing (F-P), wiping (P-T), and a 2nd placing (T-P) and wiping (P-T) for a repeated wipe pattern, are shown. Note that this particular pattern proceeds to the 2nd placing directly and does not terminate in flexion. *B*: plots of joint angles of the ankle, the knee, and the metatarsal joint angles against hip throughout the wipes shown in *A*. Direction of the motion is shown. It can be seen that the extent of knee and ankle motion can vary in magnitude between wipes, whereas the placing location is similar.

micromanipulator and moved through small known distances and rotations. Recovery of translation and rotation information was very good. Errors in absolute location of an IRED had a standard deviation of 1.6 WATSMART units centered on the absolute position (with no absolute offset). One WATSMART unit represents 0.1 mm. The largest rotations and translations could cause a maximum error of a 2-mm offset of the recorded position from actual position of a reconstructed rigid body point within the calibrated volume of the WATSMART camera's field of view. The relative errors in reconstructed limb-positioning for the large bullfrogs of 30-cm leg length used in this study were therefore <1% of total leg length.

The position of the pelvis and the heel of each leg in the world-coordinate system was calculated using centroid and orientation information. Assuming a coplanar structure of the thigh, calf, and astragalus, we reconstructed the whole-leg position and orientation. The assumption that the thigh, calf, and astragalus of the frog limb could be treated as coplanar was tested in dissected limbs. It was estimated that joint-angle errors introduced by this assumption were <5°. Exceptions to the coplanar assumption could occur in close flexion when the limb's overflexion mechanisms could operate (Lombard and Abbott 1907). This overflexion did not occur in the types of wiping we examined with the WATSMART system. From a reconstructed stick figure of the pelvis and legs, the joint-angle information was extracted. Reconstruction of joint angles is discussed in more detail below. A vid-

eotape of the frog's movement was also made during the experiment. The videotape was compared with the data from the reconstructed stick figure of the frog to confirm the qualitative features in the reconstruction. WATSMART data fulfilling all our reconstruction criteria were collected successfully from 10 animals after we had completed the processing and rejected records with reflections.

Kinematic analysis

ALIGNMENT AND SCALING OF DATA ACROSS FROGS AND CONDITIONS. The stick-figure data on the frog's wipes were aligned and scaled within species to approximate a "standard frog." For back wipes the data were rotated so that the pelvis-aligned box was in a standard configuration.

The data were rotated so that positions of stimuli were measured in body-centered coordinates. If the data from two frogs or the data from different recording sessions were to be compared, we scaled the recorded data so that body, thigh, and calf length had identical mean values in the two collections of wipes. In the data from video recordings, the records were rotated so that the pelvis-aligned box had a fixed orientation. For the WATSMART recordings of hindlimb wipes, the data were rotated so that the array frame of the pelvis, or the pelvis-aligned box, had a fixed orientation (i.e., we chose a body-centered coordinate system). The data were then scaled so that the thigh and calf had similar mean lengths when frogs were compared.

RECONSTRUCTION OF JOINT ANGLES. With planar video records, we used the relative joint angles as given by the vector cross products of the direction vectors of the adjoining segments. (See Fig. 1.)

With the WATSMART recordings, a set of joint coordinates was constructed by the following operations. (See Fig. 2, *B* and *C* for diagram.) A vector was constructed from the hip location (E) to the centroid of the pelvis IRED array (direction vector EA). This vector was used to define a perpendicular plane p1 EA. As an azimuth for the leg angle, we took the angle of the projection of the thigh direction vector ED onto the plane p1 (vector Ab) with the projection (Aa) in the same plane of the cross-product of the two hip-to-centroid vectors. The angle between the vector EA and the thigh's direction vector ED was taken to be the elevation of the leg. Rotation of the thigh/calf plane about the axis defined by the thigh's direction vector was the third rotation, necessary to define an angular coordinate system for the hip. The plane p2 perpendicular to thigh direction vector ED was defined. The cross product of DE with DC (vector Dc) was projected onto p2 (vector Ef). The angle of this vector with an arbitrary fixed vector Ed was taken to be the rotation. Ed was chosen when the frog was relaxed and in the flexed sitting posture. This coordinate system is illustrated in Figure 2C.

ERROR ESTIMATION. Errors were estimated by assuming a normal distribution of digitization errors radially about an actual location in two or three dimensions. WATSMART data had a standard deviation of ~ 1 mm. Video data had a standard deviation estimated at ~ 5 pixels (~ 1 mm), including the ambiguity in locating the joint centers. These errors could then be translated into joint-angle uncertainty, depending on link lengths and reconstruction method. A 5-pixel error translates into an error of 0.08 radians in joint angle for a link length of 2.5 cm (125 pixels).

TRAJECTORY CALCULATIONS. For the WATSMART data we calculated three-dimensional trajectory parameters. Using the Frenet-Serret formulae, we measured tangential velocity, acceleration, path curvature, and torsion for the moving joint centers and for the tip of the hindlimb during hindlimb-hindlimb wiping. The typical velocity profiles obtained are shown in Fig. 12B.

Choices of wiping phase for detailed analysis

We restricted detailed analysis to postures and trajectories in which the limbs moved freely and were unconstrained by interactions with the environment. These motions are more easily and directly related to underlying motor commands. The placing posture in both back and hindlimb wiping is the result of unconstrained motion and was utilized in comparing strategies and performance of frogs. In back wipes placing could be identified by a cessation of the motion of the limb at the most caudal extent of the motion of the endpoint. In hindlimb-hindlimb wipes, we chose the placing location on the basis of a cessation of motion with effector limb and target limb closely juxtaposed.

PRECISION MEASURES FOR THE WATSMART DATA. The similarity of motion between wipes was calculated using a statistic based on the mean deviations of endpoint postures at a stopping point in the wiping trajectories, such as placing. Some phases of wiping were found to be stereotyped. For these phases, unconstrained motions ceased at a similar point in body coordinates for each wipe within the estimated error of the recording techniques.

REGRESSIONS AND DISTRIBUTIONS TESTS. Regressions and correlation coefficients were calculated for the data with the use of standard formulae under assumptions of normal distributions of errors. As shown in the results, assumptions of normal distributions in the data were rarely violated. The MINITAB statistical package running on a Vax workstation was used for analysis.

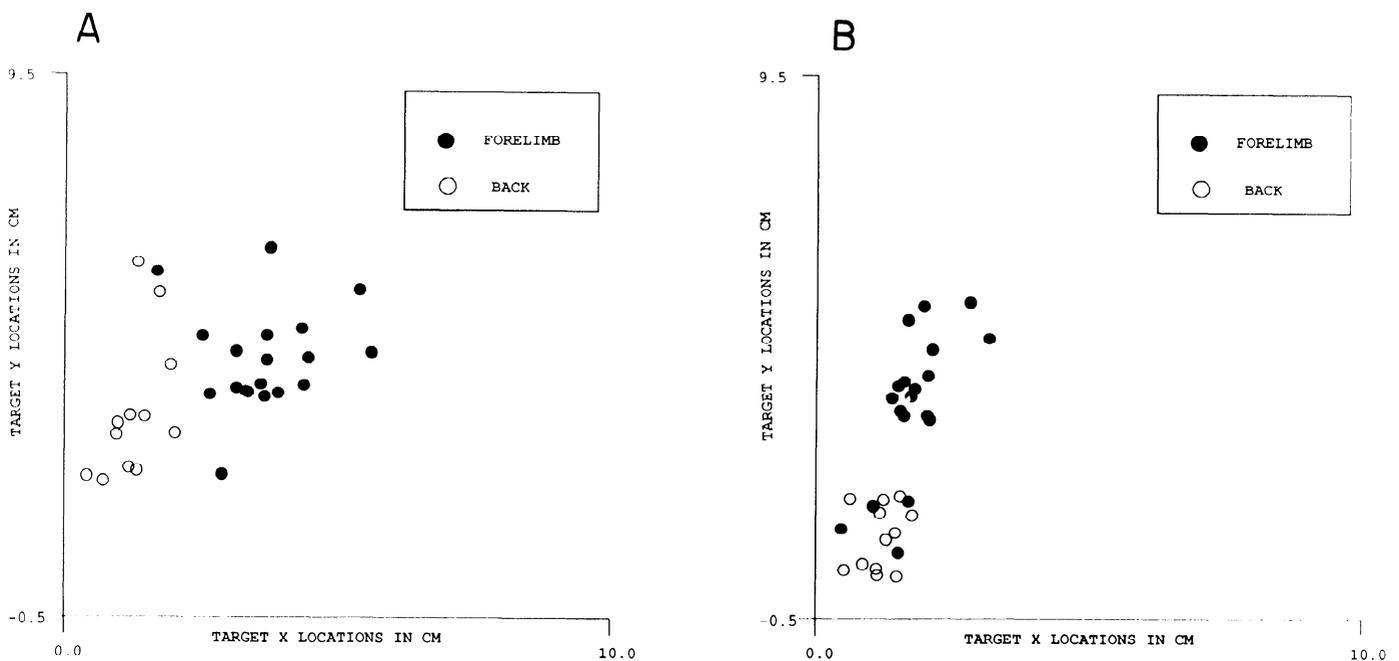


FIG. 6. *A*: spatial locations of the forelimb and back targets in a set of 5 spinal frogs, rotated and scaled in the pelvis-based coordinate frame. These form a fairly continuous distribution on the back and forearm. The frog's body length was 8 cm. Refer to Fig. 4 for the approximate scaling of this data. *B*: spatial locations of wiping limb-tip in the placing posture for the same back and forelimb wipes as in *A*. These locations form 2 clusters. Back wipes have a caudal cluster. Frogs wiping the forelimb sometimes also move the limb-tip here before stopping at the shoulder. However, most forelimb wipes involve a placing at the shoulder even after a placing at the pelvis. Specific association of placing with the later trajectory was not observed.

posture the metatarsal angle is $\sim 120^\circ$, the angle of the ankle 60° , the angle of the knee 20° , and the hip angle $10\text{--}20^\circ$. In multiple wipes, this phase may be omitted.

2) **Placing:** The wiping hindlimb is then flexed at the os cruris to astragalus (ankle) joint. Meanwhile, the metatarsals and the knee may be flexed and then slightly extended while a hip rotation and abduction brings the foot over the back. Note that, for geometric reasons, the final slight extension of the metatarsals and knee is quite significant in positioning the foot tip on the back. The limb often pauses in this posture for up to ~ 30 ms. This has been called "placing" by Berkinblitt et al. (1984).

3) **Aiming:** When the foot contacts the back, the frog then begins the wipe proper. The foot moves over the back to the target irritant, where the foot may pause. This pause has been labelled "aiming" (Fukson et al. 1980). It is seen

most easily in experiments at low temperatures. In our experiments at 20°C , aiming pauses were brief or unobservable (< 10 ms).

4) **Whisk/wipe:** In the wiping movements a whisking extension of the ankle, metatarsal joint, knee, and hip removes the irritant. (This is called the "whisk" phase.) Note that, in some instances, wiping may only involve extension of the ankle and metatarsal joints. This simpler motion may be followed by a rapid extension involving both the knee and hip or by an immediate return to the flexed posture.

FORELIMB WIPES. Wiping to the forelimb is harder to elicit than wiping to the back, especially in intact frogs. We distinguished the same four phases as seen in wiping to the back. The stimulation was placed on the dorsal forelimb at

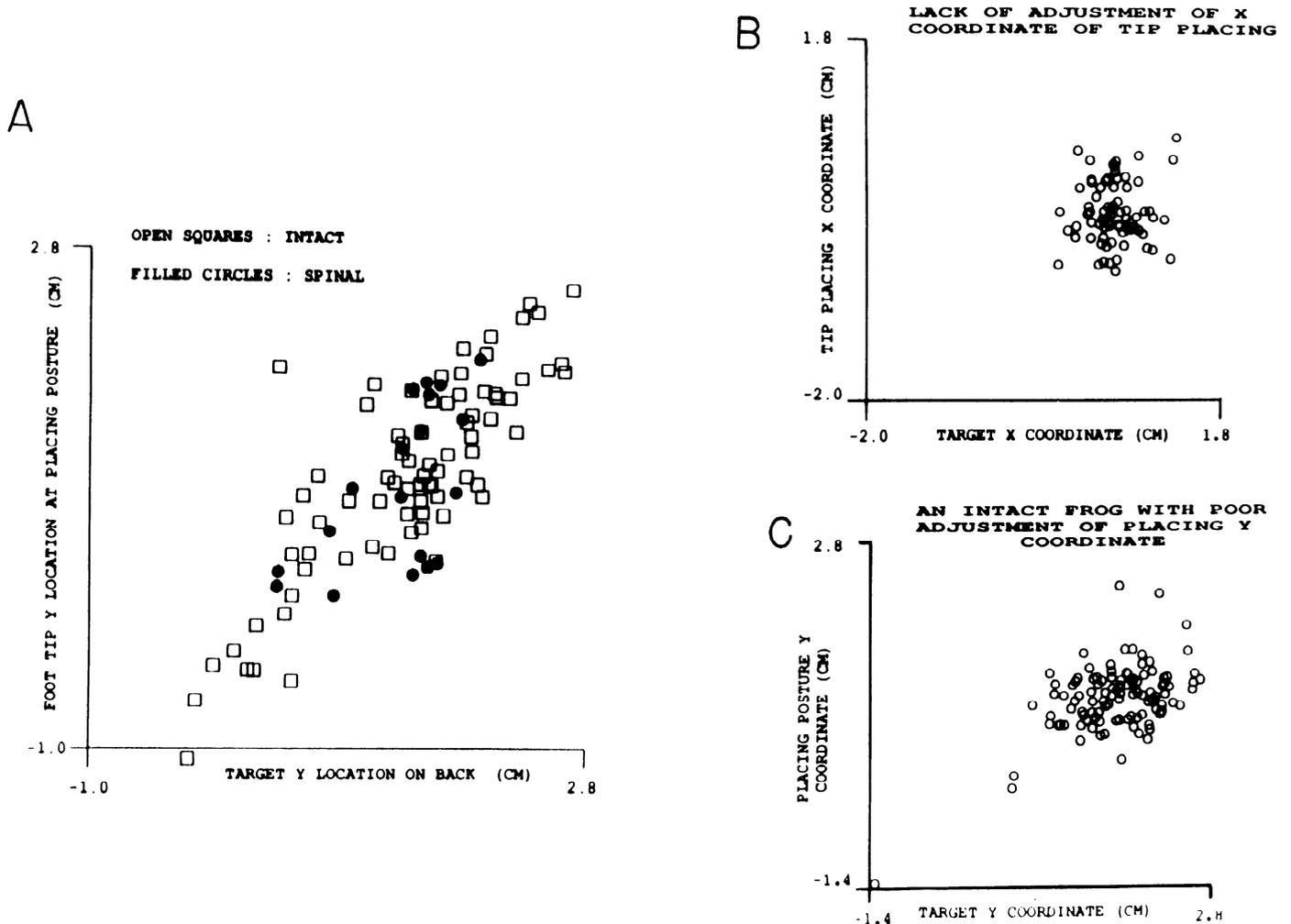


FIG. 8. *A*: relationship of the rostrocaudal location of the limb tip in placing during back wipes to the rostrocaudal location of the target in an intact frog. This could be found in almost all frogs, and the correlation coefficient was usually ~ 0.68 as in the data displayed here, with a regression slope of 0.9. Center of the pelvis is at (0, 0). Spinal data for the same animal is superimposed over intact data. Intact data are shown by the open squares. Spinal data for this same animal are shown by black filled circles. Foot-tip locations were drawn from similar distributions. (Typical results of *t* test for rostrocaudal tip positioning: $t = 0.54$, with degrees of freedom 32.3.) Spearman rank correlations of tip-to-target stimulus position both before and after operation were significant at the 0.1% level. Linear correlation coefficient of the spinal data shown here was 0.34, and the regression slope was 0.84. Data from this animal is also summarized in Table 1. *B*: apparently random distribution of the placing location in the X or lateral dimension in intact back wipes in the same data shown in *A*. Center of the pelvis is at (0,0). *C*: an exception: the placing tip-to-target relationship in 1 intact frog, which showed a far poorer Y or rostrocaudal adjustment than most frogs (as typified in *A*).

TABLE 1. Spearman rank correlations for frog A*

	Correlation	t value	P	Degrees of Freedom
<i>Preoperation</i>				
Placing XY to target XY				
Placing to stimulus Y	0.763	13.5	<0.001	76
Placing to stimulus X	0.003	0.026	>0.9	76
Joint to placing Y coordinate				
Hip	0.3379	3.12	<0.01	76
Knee	-0.6925	-8.5	<0.001	76
Ankle	0.3871	3.65	<0.001	76
Metatarsals	-0.8520	-14.37	<0.001	76
Joint to target Y coordinate				
Hip	0.455	4.45	<0.001	76
Knee	-0.493	>4.93	<0.001	76
Ankle	0.548	5.7	<0.001	76
Metatarsals	-0.773	-10.62	<0.001	76
<i>Postoperation</i>				
Placing XY to target XY				
Placing to stimulus Y	0.559	5.25	<0.001	17
Placing to stimulus X	0.198	0.622	>0.5	17
Joint to placing Y coordinate				
Hip	0.382	1.70	<0.2	17
Knee	-0.190	-0.797	<0.5	17
Ankle	0.575	2.897	<0.01	17
Metatarsals	-0.366	-1.62	<0.2	17
Joint to target Y coordinate				
Hip	0.738	4.50	<0.001	17
Knee	-0.094	-0.38	>0.7	17
Ankle	0.035	0.14	>0.8	17
Metatarsals	-0.854	-6.76	<0.001	17

* As shown in Figs. 8-10.

or near the elbow. We examined forelimb wipes in free-moving spinal frogs and in spinal frogs restrained by plastic cuffs about the wrists and ankle. Wipes were difficult to elicit in firmly restrained frogs.

The kinematics of wiping movements to the forelimbs are very similar to the back wipes until the placing posture. However, in forelimb wipes, placing generally occurs in a more rostral position and close to the shoulder. The transition from a placing to an aiming motion seen in back wipes is also seen in forelimb wipes. This transition is especially frequent when the hindlimb is positioned more caudally in the placing phase (in the area of the back normally used for back wipes).

The effect of this is to produce two clusters of placing locations for the tip (Fig. 6, A and B). The target forelimb is moved into either a lateral or caudal and extended position during the placing and aiming phases. The wipe consists of a whisking motion similar to the back wipe if the forelimb is caudal to the shoulder. A strong lateral extension is seen if the forelimb target is posed more laterally.

Similar adjustments to imposed forelimb positioning have been previously reported (Fukson et al. 1980). We observed that unrestrained spinal frogs almost exclusively used one of these two positions of the forelimb during hindlimb wiping of an unrestrained forelimb. Rigid immobilization of a forelimb with a plastic cuff could lead to misses or the absence of wipes in spinal frogs. This result

was seen when the limb was held in different postures from those seen normally but that were still in the workspace of the hindlimb. The foot surface used to wipe is sufficiently large that forelimb postures close to the normal postures could, in principle, be wiped without fine adjustment of movements. From these data alone we feel unable to assess exactly how fine-grained the adjustment of hindlimb motor-commands to variations in forelimb position may be in spinal frogs.

HINDLIMB WIPES. The wiping of one hindlimb by another involves stages that can be compared with the stages seen in the other two types of wipes.

1) Flexion: Both limbs are flexed. In repeated wipes, this phase may be omitted.

2) Placing: The limbs move to a posture elevated and caudal to the flexed posture with both legs normally off the substrate.

3) Aiming: Simultaneously, the frog moves the heel of the wiping leg and the skin location of the irritant on the target leg together (placing and aiming). This aiming posture is achieved by moving either the effector limb alone (when the target limb was acting as a postural support in intact frogs) or by moving both limbs (in all spinal frogs and in some wipes by intact animals).

4) Whisk/wipe: A strong caudal extension of the effector limb removes the irritant. Generally both legs are moved. This is diagrammed in Fig. 7.

TABLE 2. Spearman rank correlations for frog B*

	Correlation	t value	P	Degrees of Freedom
<i>Preoperation</i>				
Placing XY to target XY				
Placing to stimulus Y	0.791	10.66	<0.001	68
Placing to stimulus X	-0.245	2.08	<0.05	68
Joint to placing Y coordinate				
Hip	0.171	1.43	<0.2	68
Knee	-0.789	-10.58	<0.001	68
Ankle	0.505	4.82	<0.001	68
Metatarsals	-0.769	-9.91	<0.001	68
Joint to target Y coordinate				
Hip	0.364	3.22	<0.01	68
Knee	-0.701	-8.10	<0.001	68
Ankle	0.569	5.7	<0.001	68
Metatarsals	-0.716	-8.45	<0.001	68
<i>Postoperation</i>				
Placing XY to target XY				
Placing to stimulus Y	0.616	3.66	<0.01	22
Placing to stimulus X	0.420	2.17	<0.05	22
Joint to placing Y coordinate				
Hip	-0.342	-1.70	<0.2	22
Knee	-0.489	-2.62	<0.02	22
Ankle	0.047	0.22	>0.8	22
Metatarsals	-0.888	-9.05	<0.001	22
Joint to target Y coordinate				
Hip	-0.298	-1.46	<0.2	22
Knee	-0.178	-0.178	>0.5	22
Ankle	0.199	0.952	>0.4	22
Metatarsals	-0.450	-2.36	<0.05	22

* A frog with strong spinal tip-joint relationships.

Tip to Joint Angle Relationships

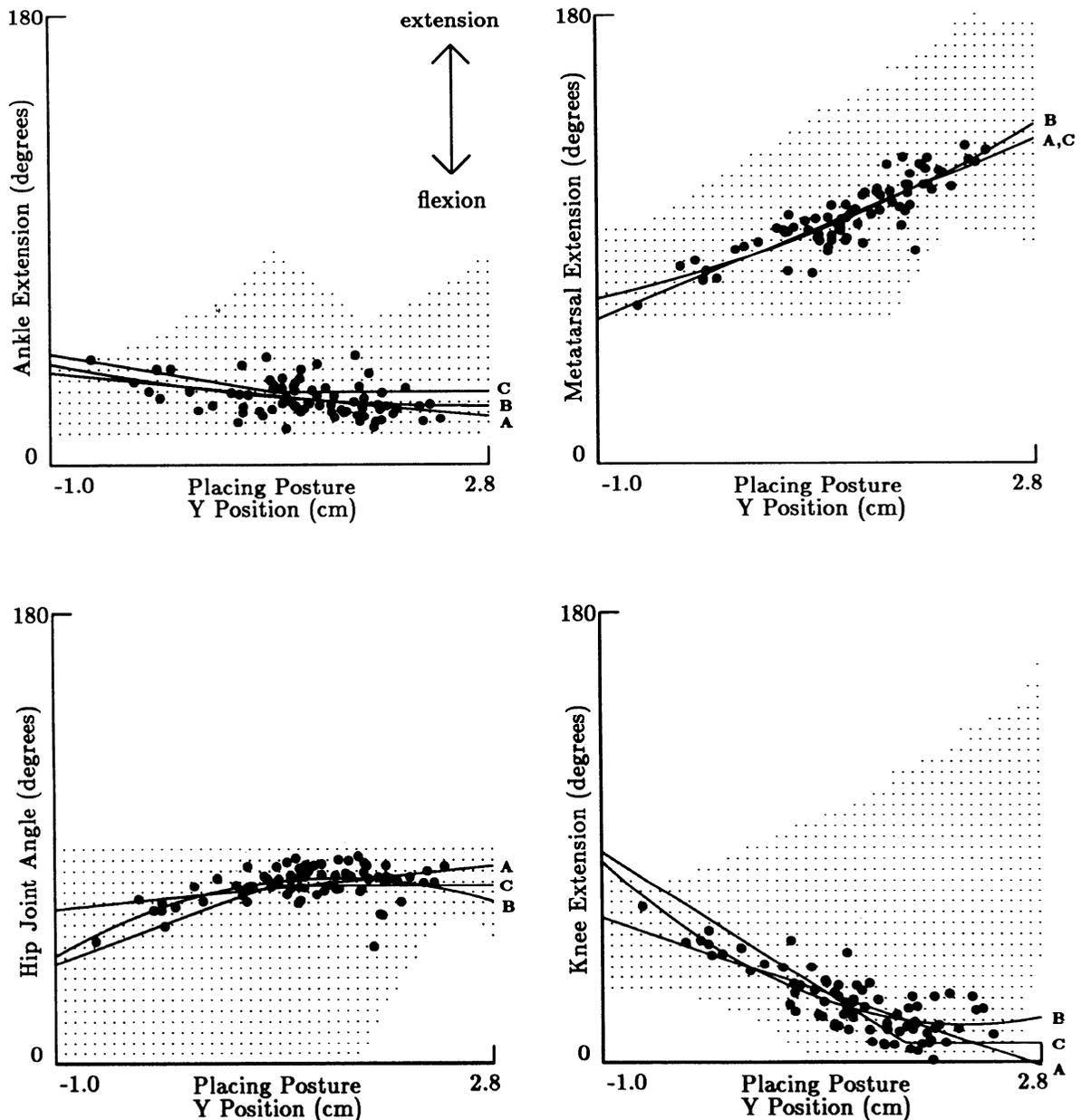


FIG. 9. Joint angles are plotted vs. tip position for the data of intact *frog 1* from Fig. 8. Stippled areas represent the possible individual joint angles that the redundant linkage could assume to reach the Y location on the abscissa. With appropriate coordination of the other joints, a particular joint angle could be selected from anywhere within the stippled region, and the tip would still be able to reach its desired location. It can be seen that the data are concentrated in small regions of the total possible stippled configuration space. Joint angles predicted by 3 simple models of the transformation are also shown. These models were parameterized using individual least-squares estimations. *Line A*: a linear choice of joint angles by an intact frog from the desired rostrocaudal location of the tip during the placing posture of back wiping. *Line B*: a 2nd-order polynomial relationship to desired tip location. *Line C*: linear choice of joint angles from desired tip location with joint limits reached in some ranges.

Quantitative analysis

SENSORIMOTOR TRANSFORMATIONS DURING WIPING TO THE BACK. To examine the sensorimotor transformations that map stimulus location into motor outputs, we exam-

ined the posture of the hindlimb with respect to the target location for the placing phase of wipes to the back. In the placing posture, the limb tip is unconstrained by interaction with any surfaces. For convenience, we defined a body-centered coordinate system for the frog to be centered

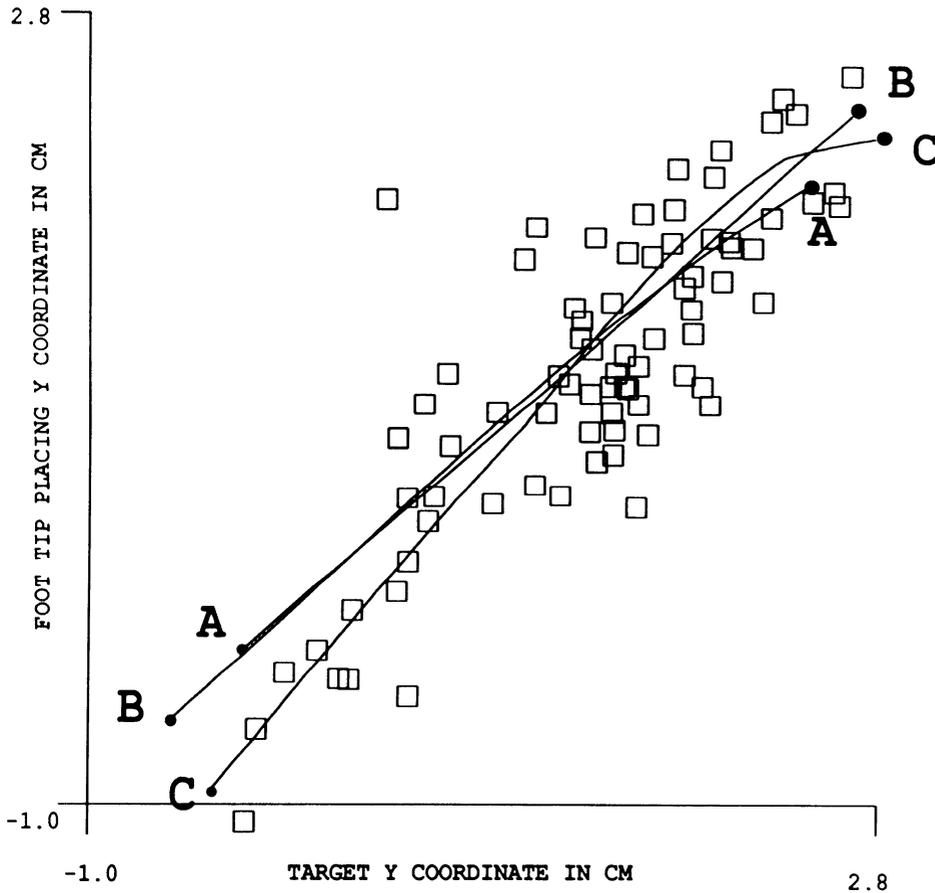


FIG. 10. Predictions of a linear, a polynomial, and a linear model with joint limits for the transformation used to adjust back wiping in intact *frog 1* (from Table 1): joint angles were estimated independently from the relationships in Fig. 9, and these values were used in a forward kinematic model to generate final tip positions. Continuous lines are the predictions: the squares are the data from an intact frog. *Line A*: a linear choice of joint angles by an intact frog from the desired rostrocaudal location of the tip during the placing posture of back wiping. *Line B*: a 2nd-order polynomial relationship to desired tip location. *Line C*: linear choice of joint angles from desired tip location with joint limits reached in some ranges.

on the pelvis with the Y axis aligned with the spine. Target positions were approximately normally distributed over the back in both the X and Y dimensions. Sample data from a typical frog (*frog A*) will be presented, and exceptions to this pattern will be noted.

Mapping of skin position into foot position. 1) Intact frogs. The distribution of placing positions of the tip of the wiping leg covered a sizable area of the body surface.

Typically, we found that there was a clear and continuous relationship between the Y coordinate of the limb tip during placing and the Y location of the stimulus. (For *frog A* in Fig. 8A, the correlation coefficient is 0.68). The placing position of the limb tip was continuously adjusted so that it lay at a fixed distance posterior to the stimulus position. This adjustment was very close to linear. There is a one-to-one mapping in the body space or hand space between the stimulus and tip locations.

In contrast to the rostrocaudal axis, the lateral or X axis distributions showed no correlation in their relationship. A caveat is in order, however. Based on estimates of digitizing error and on the lateral extent of the data, we recognize that a relationship could be buried in the digitizing noise. This noise is great enough to swamp a correlation coefficient in data of the range found in the X dimension (Fig. 8B).

Not all frogs demonstrated this precision of adjustment. Two frogs showed poor correlation. Figure 8C displays data from an intact frog (*frog C*) that shows far less correlation of target to tip Y location during placing. This frog appears to adopt a constant placing strategy for all target

locations on the back, except when placing to extremely caudal target positions. This animal did not survive transection.

Most intact frogs (18 out of 20) show a clear continuous adjustment of the Y position of the limb tip to the Y position of the target stimulus.

2) Spinal frogs. Data for the same animals after removal of the CNS anterior to the calamus scriptorius were essentially similar to data of the same intact animal. We were not able to elicit as many wipes, however. Distributions of tip location from the intact animal and spinal animal could be fully overlapped, providing that the two stimulus position distributions were similar. The tip-to-target Y correlations of an individual frog (*frog A*) after spinalization are superimposed over the intact data of this frog in Fig. 8A.

Table 1 gives a nonparametric measure of correlation for the foot tip, the target, and the joint angles in *frog A* before and after spinalization. The hip can be seen to alter its behavior in this case, although this alteration was not routinely seen. The principal relationships seen in the intact frog are preserved in the spinal animal, however, and remain significant, although performance is degraded. Table 2 shows rank correlations from a frog (*frog B*) that showed a clear and significant preservation of both the relationship between the foot tip and the target and that between the foot tip and the joints in the spinalized condition.

In summary, spinal frogs showed a similar continuous relationship between foot placing and stimulus position to that seen in the intact frogs.

Mapping of stimulus skin position into joint coordinates.

1) Assessment of redundancy. To test whether the frog's hindlimb is truly redundant during wiping, we examined the range of joint angles observed during placing. We computed the possible angles that a single joint can have that are compatible with each tip position, assuming an appropriate choice of the other joints. The angles chosen for all the other joints are constrained by the model to lie between nominal joint limits measured from a frog skeleton. In Fig. 9, the range of angle configurations possible for a tip Y position is plotted for each joint together with the observed values from an intact frog (*frog A*). It can be seen from this figure that the frog assumes a much smaller range of angles from the space of possible configurations than the redundancy would allow.

2) Joint-angle transformations. Because of the redundancy of the limb, it might be possible for the frog to fix one or more of the joint angles for all possible tip locations or even ignore control of a joint altogether. However, we found that none of the joint postures is either fixed or randomly associated with target location. Correlations between each joint angle and the target Y location show that each joint is adjusted to target Y variations (Table 1, *frog A*). Because the joint angles are potentially completely independent of target Y location, these correlations cannot be because of the kinematic interrelationships in the linkage. (These interrelationships might be supposed for the correlations with tip position.)

Figure 9 suggests that the selection of joint configuration for a given target location by the frog could be based on very simple relationships between joint angles and the desired tip location. The simplest such relationship would be

one in which each joint assumes an angle that is a linear function of the tip Y location, independent of the other joints. We modeled the results of such a transformation by performing a linear regression of joint angle to tip Y location for the observed placing postures. These regression results are shown as lines marked A in Fig. 9. We then tested the competence of this model by the use of the joint-angle values it generated to predict the relationship between target and tip location. The predicted values were compared with those actually observed. The predicted relationship is plotted as *line A* in Fig. 10. Whereas the model captures the major relationship, it does not fit the observed data well at low values of Y.

The relationship between joint angle and tip location is not necessarily linear. However, there was no significant improvement in the model if we used a second-order polynomial regression to describe the relationships of joint angles to tip position and of tip position to target location. Second-order terms for all joint relationships except the hip were not significant. These regressions and the resulting tip-to-target relationships are shown by the lines marked B in Figs. 9 and 10. Regressions with higher order polynomials (up to order 4) did not improve the fit of tip Y to target Y.

Another description that better captures the relationships of tip to target is suggested by the data for the hip and the ankle in Fig. 9. The scatter plots of joint angles to tip position for both of these joints appear to flatten out for higher values of tip Y location as the joint angles get close to the nominal joint limits. This result suggested to us that the joints might be approaching a compliant anatomical limit. A linear relationship can be used to describe the

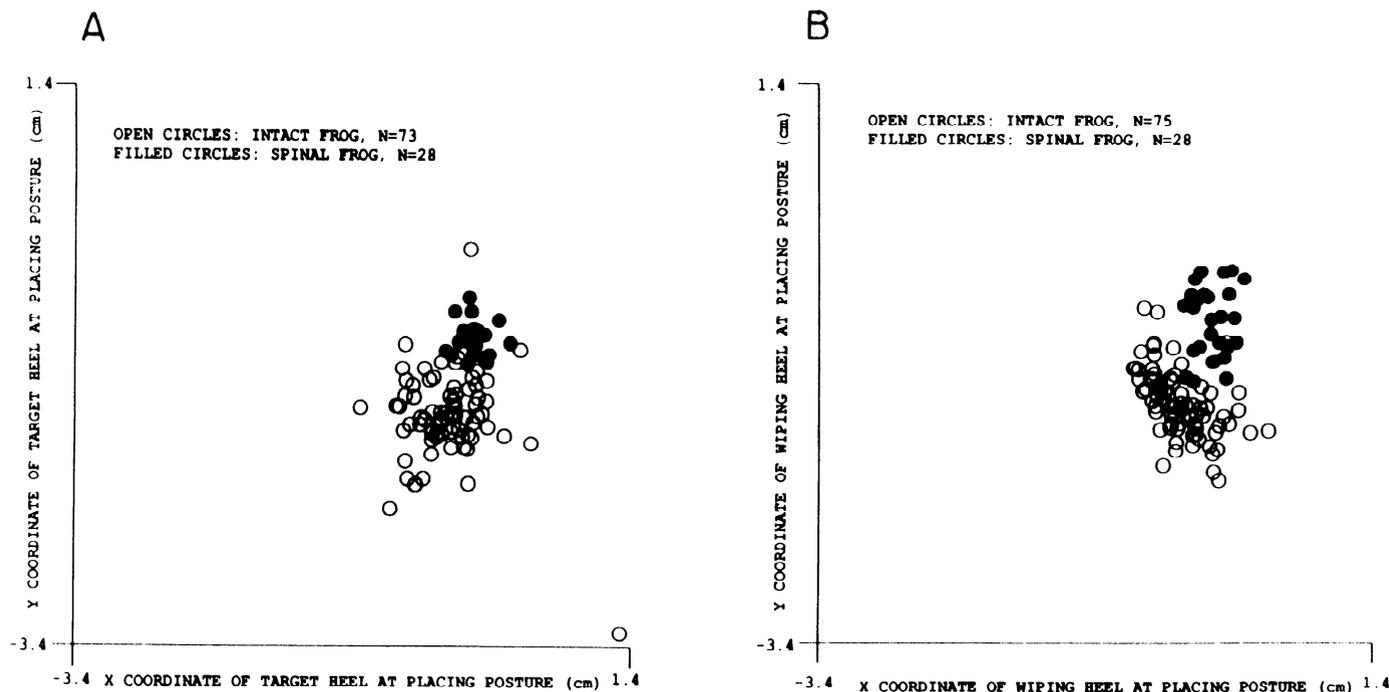


FIG. 11. Workspace coverage in the same frog when intact and spinal conditions are compared for hindlimb wiping. Location is changed, and variability is considerably and significantly reduced in the spinal condition. A: target heel's position at the placing posture. B: wiping heel's position at the placing posture. Open circles are the intact animal. Closed circles are the spinalized animal.

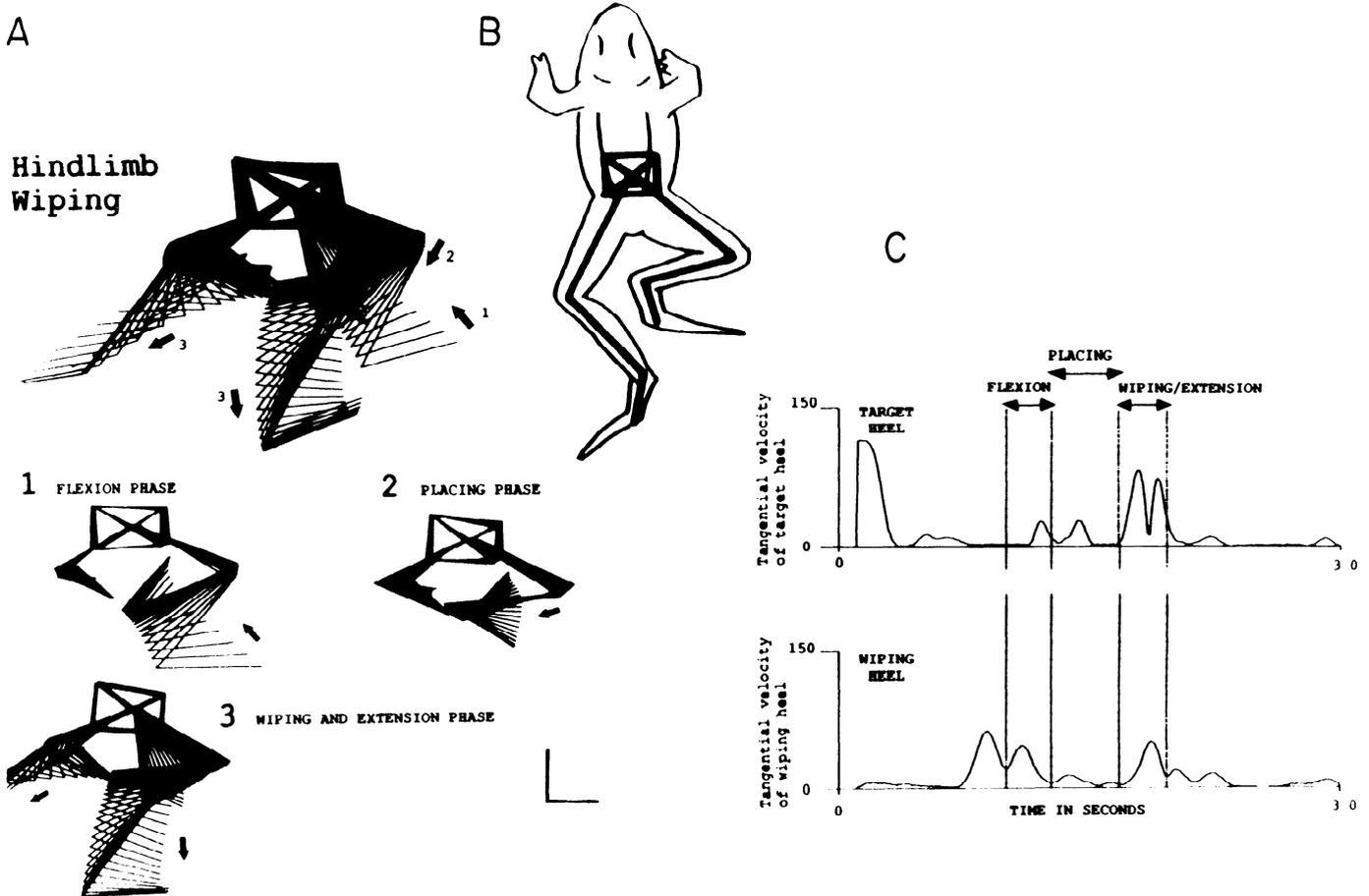


FIG. 12. Stages of wiping in a spinal bullfrog recorded with a WATSMART system at 100 Hz are displayed as successive stick figures. *A*: 1) flexion: limb is flexed into a standard posture; 2) placing: 2 limbs are elevated from the substrate and brought into close proximity; and 3) wiping: wiping limb is extended, and on some occasions such as here, the target limb is also extended. A 2-cm scale bar is shown for the lower 3 figures in the *bottom right*. *B*: schematic of a frog, which relates the stick figure shown to the body parts. *C*: tangential velocity profile of the heels of the wiping legs and the target legs seen in *A* (velocity is in centimeters per second).

desired tip-to-joint transformation. The linear relationships of joints near limits are then clipped or modified when the resulting joint angle exceeds the limit. The results for this type of model (lines marked C in Figs. 9 and 10) are in better agreement with the observed data over the full range of target Y locations. The ankle and hip become fixed at a limit for desired placing postures greater than ~ 1.2 cm.

In summary, the transformation from a desired tip position to the joint angles can be described by a simple independent linear adjustment of the joint angles, subject to constraint by joint limits in some ranges of desired tip positions. This adjustment is made possible by the frog's placing the limb in a configuration in which the transformation of joint into tip location is very close to linear.

SENSORIMOTOR TRANSFORMATIONS IN HINDLIMB-HINDLIMB WIPING. In hindlimb-hindlimb wiping, the frog has the additional freedom to position both the stimulus and effector when executing a wipe. Thus we examined hindlimb-hindlimb wipes to assess 1) whether kinesthetic information about limb configuration is used to modify the wiping trajectory, and 2) whether a continuum of different

motor equivalent solutions is used for the same target location on the skin.

1) *Intact frogs.* The stimulus was always placed on the heel of the target leg in hindlimb experiments, i.e., at a fixed location on the skin. The target and wiping hindlimbs could be in many different locations in the workspace, however. The intact frog had a preferred region for hindlimb wiping. Both limbs were normally moved to this region, but a frog would occasionally wipe freely throughout its workspace (Fig. 11A). In particular, this outcome resulted if the target limb was being used as a structural support for the body or if the animal was restrained or grasped at the ankle. A relationship was seen in the relative lateral positioning of the two limbs' heels in the placing posture. A relationship was also observed in the hip angles. However, no simple relationship existed of the type seen in the wiping to the back.

2) *Spinal frogs.* In contrast to the results for intact frogs, the spinal frog showed a hindlimb-hindlimb wiping movement with considerable stereotypy, especially in target-limb placement. (See Fig. 11.) The workspace coverage was very different from that of the intact frog. The two sets of coordinates in body space could be shown to be drawn

from very different distributions. (For example, for the t test of the rostrocaudal coordinates for the frog in Fig. 11, $t = 10.43$, and $P < 0.001$, with degrees of freedom equaling 46.) Variances of these distributions were also very different (e.g., target heel rostrocaudal standard deviation intact 17.7, spinal 6.76).

This clustering and contraction of the tip locations used in the spinal frog's placing posture suggests that this stage of wiping has been reduced to a fixed strategy in the spinal animal. To examine this hypothesis, two predictions were considered: 1) It would be expected that if a fixed strategy were used, the strategy would have reasonable precision, and repetitive wipes would have to be similar in order to be successful; and 2) if the strategy were fixed, then we would expect either that there would be no adjustment (i.e., the target would be missed) or that adjustments would be inappropriate in response to perturbations.

We carried out two sets of experiments. To examine the precision of spinal frog's hindlimb wiping, more accurate recordings of the wiping movements were made using a WATSMART system. To address the second question above, the effect of restraints and perturbations on hindlimb wiping were examined.

Precision of bullfrog spinal hindlimb-hindlimb wiping. Trajectories of target and wiping hindlimbs were recorded using the WATSMART system as described in METHODS. A typical hindlimb wipe and its component stages are shown in Fig. 12A. This motion involved no collision with the substrate during placing or the initial wipe. The paths and tangential velocity profile of the paths made by the wiping leg's heel and the target leg's heel are shown in Fig. 12B. The heel is judged to be the wiping tool from the contact to the stimulus. The wiping heel's motion consists of fairly straight movement segments, each with a unimodal velocity profile. The tip of the foot follows a more complex course. Both limbs are moved to the placing positions, and phasing of the two limbs is coordinated.

For wipes to the heel, multiple repetitions of the path of the wiping heel pass through postures at the same locations in the workspace (Fig. 13). In these multiple wipes, the final position in flexion and the postures taken in placing differ only in very minor ways (Fig. 13). The actual kicking/wiping trajectories diverge from one another, but we were unable to relate these variations to the location or configuration of the wipe or the target limb in a sample of 28 wipes. In other velocity profiles, we occasionally observed collisions of the legs with one another or the substrate. The repeated similarity between the placing motions' paths and the postures described are particularly significant because the limb is away from joint limits and is unconstrained by the substrate or the other limb. The spinal frog thus seems to produce wipes with fixed, accurate, and repeatable postures in critical phases of the wipe and to bring both limbs to a specific location in relation to the body. Only a few times in ~ 100 wipes of this type did we observe a miss under circumstances of free movement.

Lack of adjustment of spinal hindlimb-hindlimb wiping. Spinal bullfrogs recorded by the WATSMART system were next stimulated in the same way as described above, but, either before or after the commencement of wiping movements (flexion phase), the target limb was perturbed to various locations. We accomplished these perturbations

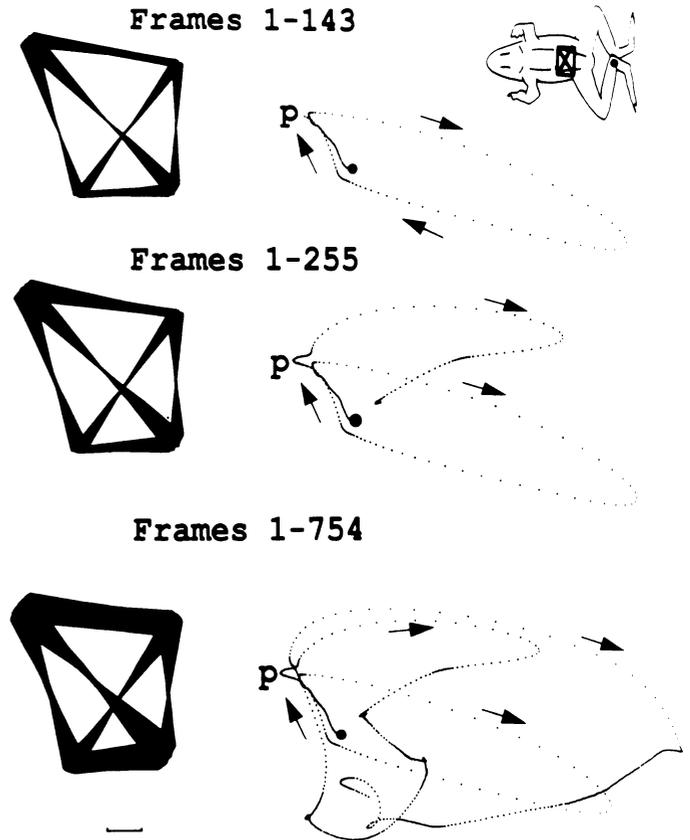


FIG. 13. Repeatability of wipes in spinal frogs. Three successive wipes of a spinal frog were recorded with a WATSMART system. These wipes (in body-centered coordinates) are displayed so as to show the close heel-placing trajectories and final heel-position region (p) utilized by the spinal frog. Note also the closeness of 2 of the wipes (2 and 3) in the initial extension phases. An illustration of the relation of the displayed markers to the frog body is shown in the *top right*. Scale bar is 1 cm.

with the use of a cord attached to the WATSMART frame on the astragalus (heel) of the target leg and threaded through the base on which the frog was mounted. The intact frog could wipe or kick effectively when the target limb was perturbed in this way. However, in the spinal frog, the effect of the perturbation was to terminate the wipes. No corrective adjustment was seen (in 30 wipes made by 5 frogs). Very small perturbations led to normal unadjusted wipes. Normal full wiping responses were observed in unrestrained control trials immediately before and after the perturbed movements.

This experiment was also repeated with five leopard frogs with the target limb restrained by a plastic cuff. Using the cuff, we pinned the limb in various locations in relation to the body. An example of such an experiment is shown in Fig. 14. The frog wiped successfully when the limb was restrained close to the usual assumed position. As the limb was moved away from the region of normal wiping, the animal missed in several locations. Further from the wiping region, the effector leg's motions became unusual. They consisted of pronounced scissoring motions of the hindlimb across the midline with the knee fairly rigid. This motion moved the effector away from the target in some cases and had no systematic relationship to limb configuration beyond the distance of the target from the normal placing zone. The movement did not proceed to the exten-

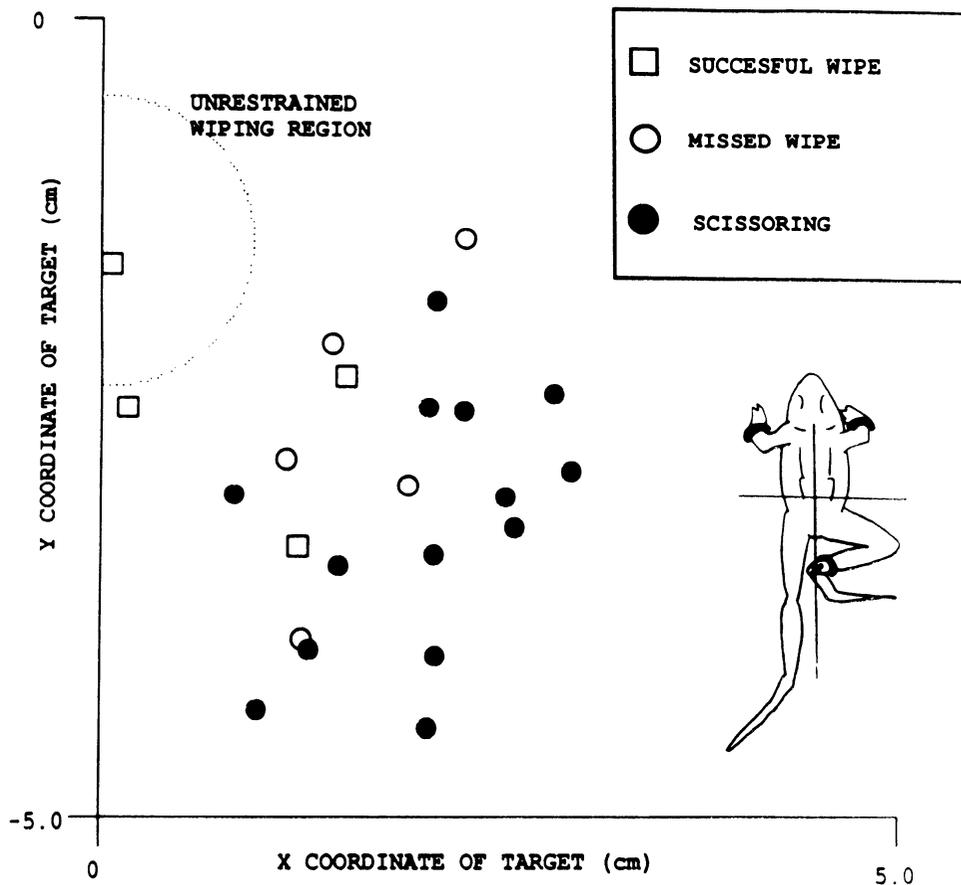


FIG. 14. Changes in hindlimb wiping and success as a result of perturbation away from the region of preferred placing. Illustration in the *bottom right* summarizes the experiment and axes displayed. Limb of a spinal leopard frog was immobilized away from the normal wiping region (this is shown as a dotted half-circle). Forelimbs and target hindlimb were restrained with tight cuffs. Y axis of the coordinate system lies along the dorsal midline. At a certain distance from the wiping region, misses (\circ) occur. Beyond this region, a scissoring movement is exhibited by the frog. This motion may even move the heel away from the stimulus.

sion and wiping phases. These are the phases that normally have the effect of removing the stimulus, so wiping failed.

These results are quite similar to those of Chepelyugina (1947), who also observed termination of hindlimb wiping in extension. Hindlimb wiping in both leopard frogs and bullfrogs thus appeared to be accomplished using a fixed strategy for a fixed skin location. Wiping seemed to be aborted if the target was far from the placing zone.

DISCUSSION

The computational approach to neuroscience attempts to classify computational solutions needed for completing tasks (Hildreth and Hollerbach 1985). To understand what the frog might be doing during wiping, it is useful to examine the types of sensorimotor transformations and associated movement strategies that are adequate to achieve the task of wiping (Berkinblitt et al. 1986; Loeb 1986). The wiping tasks involved in removing stimuli from the forelimb, the hindlimb, or the back can have many possible types of solutions. These solutions will generate different kinematics and can therefore be distinguished in experimental results. Such solutions are best examined in the unconstrained motions.

Different competent wiping strategies

Sensory information could conceivably be used in either a discrete or continuous fashion in generating wiping movements. These possibilities yield two distinct forms of sensory transformations for the wiping task.

1) *Discrete solutions.* In this type of solution, a single feed-forward program for each wipe is triggered by any

stimulus within an area of body surface. Barring mishaps, this program is guaranteed to reach every point in the area in each wipe. Many stimulus positions and configurations of the body give rise to a single strategy. Such programs can also be chained together to generate a series of movements and postures in a finite automaton arrangement.

2) *Continuously adjusted solutions.* In this class of solutions, a motor program is used in which the parameters are adjusted based on stimulus location according to a one-to-one map. Thus, for a given location, a single strategy is used in multiple wipes to a particular location, but, for a stimulus in a closely adjacent area, a similar but slightly different fixed strategy is used.

Evidence supports a discrete set of strategies in spinal turtles with a continuous adjustment of each of these strategies in the skin zones within which it is elicited (Mortin et al. 1985; Robertson et al. 1985). The evidence provided here also supports continuous adjustment to the position of the stimulus on the skin. The frog preparation allows quantitative examination of such a continuously adjusted strategy in wipes to the back made by both intact and spinal frogs. Small variations in stimulus position produced small variations in placing posture.

When a limb or manipulator has excess degrees of freedom (i.e., is redundant), the conceivable motor output for wiping can be subdivided into two classes:

1) *Fixed solutions.* In this case, a given stimulus will always produce the same motor program. The redundancy of the system may be used to optimize other aspects of performance, but this choice of free parameters does not vary for trials to the same target.

2) Motor equivalent solutions. In this class of solutions, a number of different programs may be used for each stimulus location. There is a many-to-one map of postures and movements to a given target location (motor equivalence). The program may use two different kinematic patterns under identical circumstances of stimulus location and body configuration.

Combining the above two sets of distinctions, one can divide the possible sensorimotor transformations into four distinct classes. The map or transformation from sensory coordinates to motor coordinates can be many-to-one (with a discrete use of sensory input and fixed kinematics), one-to-one (with a continuous adjustment to sensory input and fixed kinematics), one-to-many (continuous adjustment to sensory input motor-equivalent kinematics), or many-to-many (with a discrete use of sensory input and motor-equivalent kinematics). To distinguish these strategies and transformations in the frog's wiping behaviors, it is important to understand the factors that can influence the form of the kinematics.

Our evidence from unconstrained movements supports a fixed solution in intact and spinal frogs as they wipe the majority of the back. In the transition zone between back/cloacal wiping and back wiping, two discrete motor equivalent solutions exist. However, we did not see a continuous set of motor equivalent adjustments in the major skin zone where back wipes occurred, although the linkage redundancy would allow such adjustment.

Factors influencing the kinematics of the wipe

To simplify interpretation of the results in this paper, we have focused on the kinematics of unconstrained motions that are solely because of the interaction of muscle commands with muscles and with limb dynamics. The sensorimotor transformation is thus relatively direct in these cases, and the different possible strategies can be distinguished. The placing phase of movement in both back wipes and hindlimb-hindlimb wipes involves free movement of the foot through space. By contrast, the aiming phase is the result of a sliding motion along the surface of the skin.

Measuring surface interactions and limb stiffness experimentally is very difficult, even in organisms that are larger and more cooperative than frogs. Sensorimotor transformations in the kinematically constrained wiping motions may also involve reflexes that use the afference from surface interactions and are therefore more complex. For movements interacting with surfaces, then, it is difficult to distinguish between *equifinal* and *motor-equivalent* solutions, as defined by Berkinblitt and colleagues (1984, 1986). Both classes of solutions produce variations in the redundant degrees of freedom for an equivalent task output. The data for unimpeded motions collected in this study support the notion that intact and spinal frogs use a simple solution for the underconstrained kinematics of wiping.

Solutions for underconstrained kinematics by the frog

The wiping frog faces Bernstein's problem. The frog has many solutions available to it because of its limb's redundancy. This problem is ill posed.

One approach to the problem of underconstrained solutions is to choose some simple subset from among the set of solutions. Appropriately chosen subsets may simplify various aspects of motor control. One way to choose a subset is to pick sets of solutions that are defined by a simple constraint between the degrees of freedom. This choice reduces the effective degrees of freedom and may assist in both forward and inverse transformations. Such a constraint could be defined by choosing a simple surface, a plane, or line within the solution space.

The solution used by the frog for back wiping seems to be a simplification of this kind. The joint angles used to move the placing posture forward along the back are constrained to a straight line in the space of possible solutions. This choice has several advantages. It is computationally simple, and it can be executed in parallel. In addition it guarantees the invertibility of the transformation. It may also simplify the muscle commands needed. Linear transformation strategies similar to those reported here for frogs have been seen in crabs (Berkinblitt et al. 1986).

In contrast to the situation described for back wiping, the kinematics of the hindlimbs do not allow simple solutions for adjusted coordination of the limb throughout the workspace. The total workspace for hindlimb wiping is larger than that for back wipes. The wiping tool is the astragalus segment in hindlimb-hindlimb wiping. In back and forelimb wipes, the wiping tool is the entire foot (including astragalus). This combination of a large workspace and a smaller tool in hindlimb-to-hindlimb wipes places greater demands on limb coordination than in either back or forelimb wiping. When the target limb's position is varied, the configuration of the wiping limb must be adjusted in a nonlinear fashion for the frog to wipe successfully. An exception is for points along the rostrocaudal midline, when simple joint-angle matching is adequate. If the astragalus segment as a whole is considered the wiping tool, there is only one surplus degree of freedom. The task of hindlimb-hindlimb wiping is thus a more stringent test of the capacities of the spinal frog's abilities to utilize and adjust to configuration information than is either back or forelimb wiping.

We were unable to explain the overall hindlimb-placing posture of intact frogs in a simple way. A complex nonlinear adjustment may be occurring in the hindlimb-hindlimb wiping. The hindlimbs must also be coordinated in a flexible way in relation to the body in many other activities such as swimming, walking, orienting, and jumping.

Differences in adjustments between intact and spinal frogs

Wiping to the back was very similar in intact and spinal frogs. Though performance was somewhat poorer in spinal frogs, the adjustment of the placing posture to stimulus location was preserved.

In the spinal frog, the motor program for hindlimb-to-hindlimb wiping did not adjust to variations or perturbations of the target limb's configuration to generate successful wipes. This type of wipe was not discussed by Berkinblitt et al. (1986) or by Fukson et al. (1980). The only type of adjustment made by spinal frogs in hindlimb wipes was premature termination of the wipe. When displaced, the limb of a spinal frog might fail to execute a given phase of a

movement if a previous phase was not completed successfully, but no systematic corrective change in the form of a given phase of wiping was seen in response to an initial configuration restraint. Fukson et al. describe successful wipes to the forelimb irrespective of its configuration. We were able to reproduce their findings with the proviso that the limb constraint was loose.

We have observed that, for wipes of the hindlimb to the forelimb, there is also a change in the posture of the forelimb concurrent with the movement of the leg. When we artificially prevented these adjustments of the forelimb, we observed wiping misses and the absence of wipes, although the frog wiped the forelimb successfully with the constraint removed. This outcome suggests that the adjustment of spinal frogs to forelimb configuration is not a fine, continuous adjustment. There may be other factors involved in these wiping failures that have not yet been explored. These results suggest that the spinal frog is not able to use configuration information in as flexible a way as is the intact frog. It seems that information about skin location can be used in a similar way in both conditions. Kinesthetic feedback may be restricted to a gating function in the spinal frog's wiping to the hindlimb.

Our results differed from those of Fukson et al. in another way: in contrast to their results, we did not find multiple configurations corresponding to a given tip position. On this point, the results of Berkinblitt and coworkers (1986) superficially do not agree with our results. However, it is worth noting that they examined the posture of aiming. This posture is constrained by the interaction of the limb with the surface of the back. Multiple solutions were found in their study. The difficulty of interpreting constrained kinematics has been noted above. In this condition, it is difficult to decide with certainty whether the aiming posture has equifinal or motor-equivalent motor commands.

Conclusions

Adjustments of placing posture to stimulus location are preserved in the wiping movements to the back made by spinal frogs. In contrast, a clear deficit and alteration of control based on configuration information is present in spinalized frog's hindlimb-hindlimb wiping.

The use of redundancy by the frog to locally linearize a nonlinear transformation and to simplify the computational structure of a motor task is an interesting and perhaps important strategy in sensorimotor transformations.

We thank Dr. F. A. Mussa-Ivaldi for discussion of earlier versions of the manuscript, Prof. J. Hollerbach for use of the WATSMART system, and the Dept. of Mechanical Engineering at M.I.T. for access to the TRACK source code.

This work was supported by National Institutes of Health Grants NS-09343 and AM-26710 and Public Health Service training grant and Whitaker Health Sciences Fund fellowship to J. McIntyre.

Address for reprint requests: S. F. Giszter, E25-S34 Whitaker College, Dept. of Brain and Cognitive Sciences, Massachusetts Institute of Technology, 77 Massachusetts Ave., Cambridge, MA 02139.

Received 9 June 1988; accepted in final form 25 April 1989.

REFERENCES

- ABEND, W., BIZZI, E., AND MORASSO, P. Human arm trajectory formation. *Brain* 105: 331-348, 1982.
- ATKESON, C. G. AND HOLLERBACH, J. M. Kinematic features of unrestrained vertical arm movements. *J. Neurosci.* 5: 2318-2330, 1985.
- BERKINBLITT, M. B., FELDMAN, A. G., AND FUKSON, O. I. Adaptability of innate motor patterns and motor control mechanisms. *Behav. Brain Sci.* 9: 585-638, 1986.
- BERKINBLITT, M. B., ZHARKOVA, I. S., FELDMAN, A. G., AND FUKSON, O. I. Biomechanical singularities of the wiping reflex cycle. *Biofizika* 29: 483-488, 1984.
- BERNSTEIN, N. A. *The Coordination and Regulation of Movements*. New York: Pergamon, 1967.
- CHEPELYUGINA, M. F. *On the Role of Affference in Active Postural Movements* (PhD thesis). Moscow: University of Moscow, 1947.
- CONATI, F. C. *Real Time Measurement of Three-Dimensional Multiple Rigid Body Motion* (Master's thesis). Cambridge, MA: Massachusetts Institute of Technology, 1977.
- ECKER, A. *The Anatomy of the Frog*. Amsterdam: Asher, 1971.
- ERDMANN, M. A. *On Motion Planning with Uncertainty* (Master's thesis). Cambridge, MA: Massachusetts Institute of Technology, 1984.
- FLASH, T. AND HOGAN, N. The coordination of arm movements: an experimentally confirmed mathematical model. *J. Neurosci.* 5: 1688-1703, 1985.
- FUKSON, O. I., BERKINBLITT, M. B., AND FELDMAN, A. G. The spinal frog takes into account the scheme of its body during the wiping reflex. *Science Wash. DC* 209: 1261-1263, 1980.
- GOLANI, I. AND FENTRESS, J. C. Early ontogeny of face grooming in mice. *Dev. Psychobiol.* 18: 529-544, 1986.
- HILDRETH, E. C. AND HOLLERBACH, J. M. The Computational Approach to Vision and Motor Control. *AI Memo 846. Artificial Intelligence Laboratory*. Cambridge, MA: Massachusetts Institute of Technology, 1985.
- KEMALI, M. AND BRAITENBERG, V. *Atlas of the Frog's Brain*. New York: Springer-Verlag, 1969.
- LACQUANITI, F. AND SOECHTING, J. F. Coordination of arm and wrist motion during a reaching task. *J. Neurosci.* 2: 399-408, 1982.
- LOEB, G. E. Commentary. In: Berkinblitt, M. B., Feldman, A. G., and Fukson, O. I. Adaptability of innate motor patterns and motor control mechanisms. *Behav. Brain Sci.* 9: 585-638, 1986.
- LOMBARD, W. P. AND ABBOTT, F. M. The mechanical effects produced by the contraction of individual muscles of the thigh of the frog. *Am. J. Physiol.* 20: 1-60, 1907.
- MORASSO, P. AND MUSSA-IVALDI, F. A. Trajectory formation and handwriting: a computational model. *Biol. Cybern.* 45: 131-142, 1982.
- MORTIN, L. I., KEIFER, J., AND STEIN, P. S. G. Three forms of scratch reflex in the spinal turtle: movement analysis. *J. Neurophysiol.* 53: 1501-1516, 1985.
- MUSSA-IVALDI, F. A., MCINTYRE, J., AND BIZZI, E. Theoretical and experimental perspectives on arm trajectory formation: a distributed model for motor redundancy. In: *Biological and Artificial Intelligence Systems*, edited by E. Clementi and S. Chin., Escom, 1988.
- PAUL, R. P. *Robot Manipulators*. Cambridge, MA: MIT Press, 1981.
- REED, E. S. Commentary. In: Berkinblitt, M. B., Feldman, A. G., and Fukson, O. I. Adaptability of innate motor patterns and motor control mechanisms. *Behav. Brain Sci.* 9: 585-638, 1986.
- RICHARDS, O. (Editor). *Marine Biological Laboratory: Formulae and Methods*. Woods Hole, MA: Marine Biological Laboratory, 1936.
- ROBERTSON, G. A., MORTIN, L. I., KEIFER, J., AND STEIN, P. S. G. Three forms of scratch reflex in the spinal turtle: central generation of motor programs. *J. Neurophysiol.* 53: 1517-1534, 1985.
- SHERRINGTON, C. S. *The Integrative Action of the Nervous System*. New Haven, CT: Yale University Press, 1906.
- SMITH, J. L., HOY, M. G., KOSHLAND, G. F., PHILLIPS, D. M., AND ZERNICKE, R. F. Intralimb coordination of the paw shake response: a novel mixed synergy. *J. Neurophysiol.* 54: 1271-1281, 1986.
- STEIN, P. S. G. The vertebrate scratch reflex. *Symp. Soc. Exp. Biol.* 37: 393-403, 1983.
- WHITNEY, D. E. The mathematics of coordinated control of prosthetic arms and manipulators. *J. Dynamic Systems, Measurement and Control* 94: 303-309, 1972.