Afferent Roles in Hindlimb Wipe-Reflex Trajectories:
Free-Limb Kinematics and Motor Patterns

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Kargo, William J. and Simon F. Giszter. Afferent roles in hindlimb wipe-reflex trajectories: free-limb kinematics and motor patterns. J. Neurophysiol. 83: 1480–1501, 2000. The hindlimb wiping reflex of the frog is an example of a targeted trajectory that is organized at the spinal level. We tested this reflex in 45 spinal frogs to test the importance of proprioceptive afferents in trajectory formation at the spinal level. We tested hindlimb to hindlimb wiping, in which the wiping or effector limb and the target limb move together. Loss of afferent feedback from the wiping limb was produced by cutting dorsal roots 7–9. This caused altered initial trajectory direction, increased ankle path curvature, knee-joint velocity reversals, and overshooting misses of the target limb. We established that these kine
matic and motor-pattern changes were due mainly to the loss of ipsilateral muscular and joint afferents. Loss of cutaneous afferents alone did not alter the initial trajectory up to target limb contact. However, there were cutaneous effects in later motor-pattern phases after the wiping and target limb had made contact: The knee extension or whisk phase of wiping was often lost. Finally, there was a minor and nonspecific excitatory effect of phasic contralateral feedback in the motor-pattern changes after deafferentation. Specific muscle groups were altered as a result of proprioceptive loss. These muscles also showed configuration-based regulation during wiping. Biceps, semitendinosus, and sartorius (all contributing knee flexor torques) all were regulated in amplitude based on the initial position of the limb. These muscles contributed to an initial electromyographic (EMG) burst in the motor pattern. Rectus internus and semimembranosus (contributing hip extensor torques) were regulated in onset but not in the time of peak EMG or in termination of EMG based on initial position. These two muscles contributed to a second EMG burst in the motor pattern. After deafferentation the initial burst was reduced and more synchronous with the second burst, and the second burst often was broadened in duration. Ankle path curvature and its degree of change after loss of proprioception depended on the degree of joint staggering used by the frog (i.e., the relative phasing between knee and hip motion) and on the degree of motor-pattern change. We examined these variations in 31 frogs. Twenty percent (6/31) of frogs showed largely synchronous joint coordination and little effect of deafferentation on joint coordination, end-point path, or the underlying synchronous motor pattern. Eighty percent of frogs (25/31) showed some degree of staggered joint coordination and also strong effects of loss of afferents. Loss of afferents caused two major joint level changes in these frogs: collapse of joint phasing into synchronous joint motion and increased hip velocity. Fifty percent of frogs (16/31) showed joint-coordination changes of type (1) without type (2). This change was associated with reduction, loss, or collapse of phasing of the sartorius, semitendinosus and biceps (iliofibularis) in the initial EMG burst in the motor pattern. The remaining 30% (9/31) of frogs showed both joint-coordination changes 1 and 2. These changes were associated with both the knee flexor EMG changes seen in the other frogs and with additional increased activity of rectus internus and semimembranosus muscles. Our data show that multiple ipsilateral modalities all play some role in regulating muscle activity patterns in the wiping limb. Our data support a strong role of ipsilateral proprioception in the process of trajectory formation and specifically in the control of limb segment interactions during wiping by way of the regulation and coordination of muscle groups based on initial limb configuration.

INTRODUCTION

Wiping reflexes in the spinal frog have been a model preparation to examine how the spinal cord generates and controls targeted limb movements (Berkinblit et al. 1986a,b; Fukson et al. 1980; Giszter et al. 1989; Schotland and Rymer 1993a,b; Sergio and Ostry 1993). Spinal frogs exhibit specific movement strategies for coping with ill-posed computational problems that arise from the kinematic redundancy of the limb (Giszter et al. 1989). Spinal frogs also have been shown to use body-scheme information to regulate trajectory formation during wiping (Fukson et al. 1980). Most wiping reflexes that have been examined (e.g., to irritants placed on the back, forelimb, and contralateral hindlimb) exhibit a modular organization in which the entire behavior can be described as a sequence of discrete movement phases (Berkinblit et al. 1986a; Giszter et al. 1989; Sergio and Ostry 1993). Wipe, scratch, and withdrawal reflexes all have been used to examine the possibility that the underlying spinal circuitry generating and controlling the behavior also exhibits a modular organization (Giszter et al. 1993; Schouenbourg et al. 1994; Stein and Smith 1996; Stein et al. 1986; Tresch and Bizzi 1999; Tresch et al. 1999).

Researchers have suggested that wiping reflexes may be constructed from combinations of force-field primitives (Bizzi et al. 1991; Giszter et al. 1991, 1993a,b; Mussa-Ivaldi et al. 1990, 1994). Force-field primitives initially were identified in spinal microstimulation studies. A force field is defined here as a function mapping limb position to end-point force. Force fields were constructed by measuring isometric forces at the ankle with the limb held in a range of positions and with the same stimulus applied at each position. Primitives were defined as force fields that exhibited invariant force vector directions and magnitude balances over time, i.e., conserved structures. Only a few primitives were found for any individual frog, and each primitive converged to a different location in the limb’s work space. Primitives were similar among frogs (Giszter et al. 1993). The effect of coactivating primitives could be described simply as the linear sum of the individually activated force...
fields (Mussa-Ivaldi et al. 1994). Theoretical studies have shown that summation and magnitude scaling of a few force-field types in principle could be used to generate a large range of force-field structures and might account for the synthesis of natural behaviors including wiping reflexes (Mussa-Ivaldi 1992, 1997; Mussa-Ivaldi and Giszter 1992). However, details of the links between primitives, pattern generators, and circuitry for reflex behaviors are still not well understood.

If primitives are combined to produce reflex behaviors, as suggested by other studies (Giszter and Kargo 2000; Giszter et al. 1993; Kargo and Giszter 2000; Tresh et al. 1999), it seems likely that feedback may adaptively regulate the phasing and amplitude of the component primitives. Thus to understand how primitives may be combined in reflex behaviors (e.g., wiping reflexes), we also must understand feedback controls and their effects during these behaviors. Existing published data are insufficient to allow such an understanding. It is critical to the development of ideas about primitives and their relations to central pattern generators to examine proprioceptive feedback effects during unperturbed wiping.

Proprioceptive feedback has been suggested to play several roles during wiping movements. First, proprioception could be used in gating, interrupting, or aborting phases of wiping movements, as suggested by data from Chrepelyugina (1947) and Giszter et al. (1989). Second, feedback is expected to regulate certain muscle properties during the movement (Nichols and Houk 1976). Loe et al. (1993) showed in spinal microstimulation studies that feedback might compensate for muscle length variations and regulate stiffness at the force-field level in the frog. Third, proprioception has been suggested to participate in trajectory formation in frogs, in the context of a lambda model of motion generation (Berkinblit et al. 1986b; Ostry et al. 1991). Finally, Schotland showed that frogs may be able to compensate for external loads added to the limb during wiping movements (Schotland and Rynner 1993b).

In contrast, other data suggest that feedback may not be necessary during unobstructed wiping or scratching movements of lower vertebrates. In paralyzed, or “fictive,” turtle preparations, scratching is elicited readily and different scratching forms can be distinguished in hindlimb neogrems without phasic proprioceptive feedback (Robertson et al. 1985; Stein 1983). Moreover, in the frog, several factors have been cited as indications for a mainly feedforward control of hindlimb movements (Loeb 1986; Simpson 1969, 1976). These include the low gain of monosynaptic stretch reflexes in reduced preparations, the relatively high ratio of muscle stiffness to limb mass, and the reduced postural requirements for the hindlimbs in frogs. However, despite these data in reduced or paralyzed preparations, it remains possible that feedback plays a substantial role during active wiping movements in the spinal frog.

In this paper, we present detailed kinematic and electromyographic analyses of the hindlimb-to-hindlimb wiping reflex. This is a specific form of hindlimb wiping where an irritant is placed on the foot of the contralateral hindlimb. We provide a detailed analysis of the wiping limb trajectory when starting from a range of initial limb configurations and test for motor-pattern variations at each position. We examine the trajectories in both intrinsic (joint space) and extrinsic (Cartesian) coordinates and relate these path variables to the underlying motor pattern. We examine the roles of proprioceptive and cutaneous feedback in regulating wiping kinematics and the underlying motor pattern by using dorsal rhizotomy (i.e., complete deafferentation) and selective cutaneous deafferentation. Such an analysis has not been reported to date. Finally, we examined interanimal variations in trajectory formation among frogs, how these variations relate to motor-pattern variations, and how these can predict an animal’s susceptibility to deafferentation.

The deafferentation data show a substantial role for proprioceptive feedback in regulating wiping trajectories. In particular the initial trajectory direction, the end-point path, and the accuracy of target (i.e., irritant) contact are all affected by deafferentation. In addition, when feedback was intact, motor-pattern features clearly were regulated based on the initial limb configuration. Removal of this feedback eliminated position-dependent changes in the motor pattern and produced specific motor-pattern changes. Finally, our data revealed differences in motor-pattern construction and trajectory formation among frogs that predicted their levels of reliance on sensory feedback (i.e., the degree of deficit after deafferentation). The manner of organization and control of trajectories by the spinal cord may be relevant to voluntary movement control and trajectory formation. In particular, the systems organizing trajectories at the spinal level might represent one of the substrates of voluntary or descending control (see e.g., Bizzi et al. 1995).

METHODS

Surgery

Adult bullfrogs (200–350 g) were anesthetized with a solution of 5% 3-aminobenzoic acid ethyl ester (Tricaine). Skin incisions were made on the dorsal neck region, and the muscle layers separated at the midline. The dorsal connective tissue between the skull and first vertebra was opened, and the spinal cord transected at the medullary-spinal cord junction. Gelfoam was placed in the lesion cavity and over the cord. A small hole was made in the dorsal skull to cauterize the tectum and forebrain. Gel foam again was placed to fill the opening. The surgical incision on the skin was closed with wound clips and sealed with cyanoacrylate tissue adhesive (Vet-bond).

Incisions were made on the dorsal and ventral thigh to implant a pair of electrodes (7-strand Teflon-coated stainless steel wire with 1 mm exposure under a wax ball) in biceps (BI), vastus externus (VE), rectus anterior (RA), semimembranosus (SM), and gluteus (GL), sartorius (SA), ventral head of semitendinosus (ST), adductor (AD), and rectus internus (RI). A modified patch electrode design was sometimes used to record from the thin SA muscle in smaller frogs. Patch electrode designs are presented in detail in Loeb and Gans (1986; e.g., see Fig. 10.6). Our design differed from those presented in Loeb and Gans (1986) in that the EMG wires were led back through the recording surface side of the patch and through the muscle. This arrangement reduced the need to suture all four corners of the patch into SA, which has a very thin fascial sheath. BI is a knee flexor/hip abductor. VE is mainly a knee extensor. RA is mainly a hip flexor. SM is mainly a hip extensor with some knee flexor action. GL is a hip abductor/hip flexor. SA is a hip flexor/knee flexor. The ST head we implant is mainly a knee flexor/hip extensor. AD is a hip extensor. Finally, RI is a hip extensor/knee flexor. The broader muscles such as SM and RI may have also multiple functional subdivisions of the muscle; these actions in the preceding text were classified by grossly stimulating the motor entry point (and see Lombard and Abbott 1990). Sites of implantation were the same between frogs. Electrode separation was designed to provide clean localized multiunit EMG without cross-talk from other muscles. This more local sampling from the muscle also necessitated some multi-trial averaging to give a
reasonably smooth rectified envelope. The wires were braided and led directly out of the incision. The incision was closed with wound clips and Vet-bond.

A laminectomy was performed, exposing the lumbar spinal cord. The dura was opened by careful electrocautery. Three large pairs of dorsal and ventral roots (7–9) carry the vast majority of peripheral afferent and efferent information to and from the lumbar enlargement of the frog. To deafferent the frog, dorsal roots 7, 8, and 9 on the ipsilateral side to the wiping limb were identified, lifted with a hook, frozen with a cold copper rod, and cut distal to the frozen area. These three dorsal roots carry the large majority of sensory feedback from the wiping limb to the lumbar spinal cord (Ebbeson 1976). Dorsal root 10, which was left intact, carries somatosensory feedback to the spinal cord, and a small number of C type afferent fibers may remain intact in the ventral roots (Della Torre et al. 1996). Nonetheless, when the animal recovered from anesthesia, there was no reflex responsiveness (as measured by EMG and video) to cutaneous stimuli, muscle palpation or kinematic manipulations to the wiping limb. To examine injury discharge in this technique, we recorded the roots to be lesioned in some deafferentations. Freezing before cutting caused a very reduced injury discharge which was silenced in ~5–10 min rather than persisting for long periods as sometimes reported. We thus reduced the likelihood of the concomitant possible injury discharge effects on spinal organization (Blenk et al. 1996, Wall et al. 1974).

In experiments where the role of cutaneous afferents was assessed, several incisions were made across the hindlimb at sites where cutaneous nerves could be dissected, identified, and cut. Light (dragging sharp forceps) and deep skin stimulation (pinching with toothed forceps) were used to assess if receptive fields remain intact (i.e., the hindlimb yielded no reflexive withdrawal or toe movements). The skin incisions were sealed with wound clips and Vet-bond.

**Video recording and EMG collection**

Movements were videotaped from above, perpendicular to the plane of the wipe. Therefore wiping movements out of the plane were not detected by video but were expected to be relatively small (see Giszter et al. 1989; Schotland and Rymer 1993a; Sergio and Ostry 1993). We will begin to address the vertical components of wiping in isometric force field and other experiments described in subsequent papers. The video record was collected from a camera with a 1-ms/field shutter operating at 30 frames (60 fields)/s. Video was synchronized to the EMG collection via an external tag [i.e., light-emitting diode (LED) emission] generated from Axoscope software.

EMGs were band-pass filtered with A-M Systems Amplifiers (100 Hz and 10 kHz cutoffs) and amplified by 1,000. Sensed EMGs were displayed on oscilloscope. Although the amplifier upper cutoff was 10 kHz, EMG frequency content in the frog is substantially lower and our records had little high-frequency noise. They were led into an Axotape display on oscilloscope. Although the amplifier upper cutoff was 10 kHz, EMG frequency content in the frog is substantially lower and our records had little high-frequency noise. They were led into an Axotape acquisition board, sampled at 1,000 Hz, a frequency appropriate for frog EMGs (see Giszter et al., 1993), and stored using Axoscope software (Axon Instruments, Foster City, CA). Because of the reduced sampling frequency of the video, there was some error in the synchrony between EMG and video due to detection of the external tag, but this was always ≤17 ms for individual wipes.

**Recording free-limb kinematic**

The frog was supported in a sculpted orthopedic casting plastic (Orthoplast) base with two horizontal platforms to separately support the hindlimbs. The arrangement allowed the hindlimbs to be positioned in a horizontal plane with the ankle as the only part of the hindlimb in contact with the surface. Wetting the Orthoplast support and the ankle skin reduced the friction at the initiation of the wipe. A pelvic clamp secured the frog on the support base and did not interfere mechanically with the wiping movement. After positioning the limb, the wiping reflex was elicited by biphasic, 1- to 2-ms voltage pulses (range 3–10 V) at a frequency of 20–30 Hz, applied for 500–700 ms through bipolar leads attached via alligator clips to the skin on the contralateral foot. The frog was allowed 3–5 min rest between stimulations to avoid habituation. A voltage and train duration was chosen to reliably elicit the reflex throughout the course of the experiment, and once again was not changed during the experiment. After a series ofafferented wipes, the frog was deafferented as detailed (see Surgery), then allowed 1–3 h to recover after the dorsal root lesions (as described in Loeb et al. 1993). The same initial positions throughout the wiping limb’s work space were then tested (see Experimental design).

**Analysis of kinematics**

Hip, knee, and ankle positions of the wiping limb were digitized from video for all experiments. Both the onset of wiping limb movement and time of target limb contact (and thus termination of the unconstrained free-limb segment of trajectory) were determined from the recorded video. This portion of the wipe was typically between 250 and 400 ms. The digitized positions were used in S-Plus statistical software package (Mathsoft, Seattle, WA) to reconstruct the ankle trajectory and joint angles during the movement.

Measures used to describe kinematic features included measures of normalized path length, initial direction of the ankle trajectory, overshoot of the ankle trajectory, peak tangential velocity of the ankle, and peak hip- and knee-joint velocities. Normalized path length was determined by dividing the total Cartesian length of the ankle path by the straight-line Cartesian distance between the start and stop locations of the ankle. Note that this measure bears no relationship to accuracy of movement in relation to the target stimulus or the frog’s body. A value of 1 would indicate a perfectly straight path (see Fig. 1). The initial trajectory direction was calculated relative to the radial direction from hip to ankle. This was determined by taking the arc-cosine of the inner product of the average initial direction (i.e., unit) vector of the wiping trajectory (a’ in Fig. 1) during the first five frames of movement and the direction (i.e., unit) vector from the ankle to the hip at the first frame (c in Fig. 1). Overshoot was defined here as the maximum contralateral horizontal deviation of the ankle past the stationary hip joint. Ideally we would refer to the overshoot from the target region where the legs meet. However this varied somewhat among frogs, and the value we used referenced to the hip allowed us to directly compare wipes between frogs of different sizes after scaling. Overshoot was normalized based on the length of the limb. Finally, peak tangential velocities of the ankle and peak joint velocities were determined by differentiating interpolated position-time data. The equations for calculation of normalized ankle path NPL and initial angle θ trajectory parameters are given in the following text

\[
\text{NPL} = \sum_{i=1}^{5} \sqrt{(x_i - x_{i-1})^2 + (y_i - y_{i-1})^2} / \sqrt{(x_5 - x_0)^2 + (y_5 - y_0)^2}
\]

Where \(x_i\) and \(y_i\) represent the time-varying positions of the ankle in the horizontal plane, \(x_0\) and \(y_0\) represent the ankle position at limb contact, \(x_1\) and \(y_1\) represent the initial position of the ankle

\[
\Theta = \arccos\left( \frac{\sum_{i=1}^{5} (v_i - v_{i-1})}{5} \cdot \frac{(v_0 - v_{hip})}{5} \right)
\]

\[
\Theta = \arccos\left( \frac{\sum_{i=1}^{5} (v_i - v_{i-1})}{5} \cdot \frac{(v_0 - v_{hip})}{5} \right)
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\]
Where \( v_i \) represents the time varying vector of the ankle at time \( i \), and therefore \( (v_i - v_{i-1}) \) is a vector representing ankle velocity, \( (v_{10} - v_{	ext{hip}}) \) represents the polar vector from hip to ankle to which the velocity is referenced. Finally

\[
\text{Overshoot} = \max (x_{\text{hip}} - x_{\text{ankle}})
\]

**Work-space division**

In the first experimental series, the work space was divided into rostral and caudal sectors and into proximal and distal rings based on a polar coordinate system centered at the hip. This was to determine regional differences in the changes of kinematic parameters after deafferentation. Wipes where the ankle was positioned between 0 and 45° vectors from the hip were included in the rostral sector. Wipes where the ankle was positioned between 45°, and larger angles from the hip were included in the caudal sector. The normalized path length and wiping direction across the work space.

**EMG analysis**

EMG data from our experiments were analyzed to determine the magnitude of EMG activity of ≤10 hindlimb muscles during the unconstrained free-limb phase of the wiping trajectory. Raw EMG signals were rectified and filtered with a 30-point tapered box car filter (Basmajian and DeLuca 1985) off-line in S-Plus (see Fig. 1B for procedure). The magnitude of rectified and filtered EMG envelopes were determined for each wiping trial by calculating the integral over the period from the onset of BI, usually the first muscle activated during wiping, up to the offset of VE, usually the last muscle activated. Thus EMG envelope magnitude is defined here as the area under the rectified and smoothed EMG signal. The EMG envelope magnitudes for an individual muscle were averaged for all wipes starting from the same initial position. In addition to looking at EMG envelope magnitudes, we looked at the latencies between the onset of critical muscles (BI or ST, usually the first detectable EMGs, and RI/SM/AD, a later activated group of muscles). We also looked at the durations of activity of these muscles (BI, ST, RI, SM, AD) during the wipe.

**Experimental design**

In all experimental series, the frog began with the limb positioned at rest on a moist platform in a configuration chosen by the investigator. Frogs were tested from each location at 4-min intervals to

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**FIG. 1.** Data analysis. A: hip, knee, and ankle position were digitized from video. Video camera was placed perpendicular to the horizontal plane of the wiping reflex. Kinematic measures were made from digitized records of the ankle path (see text). Normalized ankle-path length was computed by dividing the actual path (line a) by the straight line distance between the initial and final or contact positions of the ankle (line b). Initial direction of the ankle trajectory was averaged over the first 5 frames of movement to provide the initial direction vector (vector a'). Vector a' was expressed in a polar coordinate frame, i.e., relative to a line connecting the initial ankle position and the hip (vector c). Thus the inner product of unit vectors a' and c was used to calculate the angle of the initial trajectory. Overshoot of the ankle path was calculated as the maximal horizontal (mediolateral) distance of the ankle relative to the hip (distance d). Hip angle (H') was determined relative to the rostro-caudal axis of the body, and the knee angle (K') was internal to the thigh and calf. B: raw electromyograms (EMGs) were amplified at a gain of 1,000 times, band-pass filtered with cutoffs of 100 Hz and 10 KHz, for 8–12 muscles [rectus internus (RI) and biceps (BI) shown here in columns 1 and 2, respectively] and were A/D converted and collected on computer at 1 kHz for individual trials. These records were rectified and filtered with a 30-point tapered box car filter. EMG measures were made on the individual filtered EMGs. Collections of individual trials (8–12) for a particular condition then were averaged after they were aligned on the highly repeatable peak of RI activity.
prevent fatigue, sensitization, or habituation. As a test of this, the duration of wipes was tested for stability through a series.

For the first experimental series, wipes were elicited with the wiping limb in a number of different initial positions in the work space (12−15 positions). The target limb always was placed in the same initial posture before we elicited the wipe. The frog then received a dorsal rhizotomy of the wiping limb side and was allowed 1−3 h of rest and recovery from the lesions (Loeb et al. 1993). The same work-space positions were revisited and wiping was elicited at each. The initial limb positions were similar between frogs (n = 10 frogs) and chosen to span the reachable work space of the wiping limb.

In the second experimental series, multiple wipes (8−12) were elicited at each of three positions in the work space. These experiments identified intrainimal variability at a single position and variable motor-pattern features between positions. The positions were similar between frogs (n = 11 frogs) and included a rostral position (hip ∼ 80°, knee ∼ 120°), a caudal position (hip ∼ 130°, knee ∼ 120°), and a position that represents the normal resting posture of the wiping limb (hip ∼ 105°, knee ∼ 80°). After an initial afferented series of wipes, frogs received a dorsal rhizotomy, were allowed 1−3 h of rest, and the same positions were revisited for a deafferented series of wipes.

In a third experimental series, wipes were elicited with the wiping limb in a number of different initial positions in the work space (12−15 positions). The frog received a cutaneous deafferentation of the wiping limb and was allowed 1−3 h of recovery. The same work-space positions were revisited, and wiping was elicited at each. The frog then received a dorsal rhizotomy of the wiping limb side and was allowed 60−120 min recovery time, and wiping was elicited at the same work-space positions. We tested four frogs in this manner and compared changes after cutaneous and total deafferentation of the wiping limb.

In a final series, wipes were elicited with the wiping limb in a number of different initial positions in the work space (12−15 positions). After dorsal rhizotomy and a series of deafferented wipes from the same positions, the frog received a contralateral ventral root rhizotomy. This immobilized the target limb and prevented beta activation of target limb muscle spindles. We tested five frogs in this manner and compared changes after deafferentation of the wiping limb and after target limb immobilization by de-afferentation.

RESULTS

A total of 45 frogs were prepared, examined, and tested to provide the kinematic and motor-pattern data described here. This population of frogs was divided into several groups for specific procedures described below.

Qualitative kinematic and motor-pattern effects of deafferentation

In the hindlimb to hindlimb form of wiping, the irritant stimulus is applied to the hindlimb contralateral to the effector limb. Both limbs move in concert. They meet at a region along the midline caudal to the cloaca. The effector (referred throughout the remainder of the paper as “wiping”) limb then removes the irritant from the stimulated (referred to as “target”) limb using the heel as the wiping tool.

Figure 2, A and C, shows the typical kinematic patterns evoked by the wiping stimulus in two separate spinal frogs when sensory feedback was intact. The kinematics of the wiping and target limbs (thigh and calf of both) are expressed as sequences of stick figures, and arrows mark the progression of ankle movement. Bold stick figures represent the portion of the wiping limb trajectory from movement onset up to contact with the target limb. This targeted portion of the wiping limb trajectory forms the major focus of our analysis. Because this form of wiping was evoked by irritants placed on the contralateral limb, it still can be evoked when the wiping limb is deafferented (i.e., feedback from the target limb is still intact).

We exploit this feature to examine if the wiping trajectory and the underlying motor-pattern change as a result of deafferentation.

After deafferentation of the wiping limb, there were several qualitative changes in the trajectory of the wiping limb, which can be seen most clearly by comparing the frog in Fig. 2, C and G. First, the initial direction of the ankle trajectory (first 5 frames of movement) appeared caudally rotated relative to the region of target limb contact. Second, the entire ankle path up to limb contact appeared less straight or more curved. Third, the ankle trajectory overshot the normal target region where the limbs normally made contact. Finally, after limb contact was made, the ensuing limb extension/whisk phase appeared not as strongly activated. This phase normally serves to remove the irritant once limb contact has been made.

The kinematic changes were accompanied by qualitative motor-pattern changes. Again these can be most clearly seen by comparing the motor patterns shown in 2, D and H. First the initial period of limb flexor activation (BI, ST, and SA) became less distinct. Second, there was a collapse of phasing between this initial period and a second period of hip extensor activation (RI and SM). Third, VE activity that closely followed limb contact (second arrow; asterisk) was no longer apparent.

In comparing the two frogs shown in Fig. 2, A and C, it appeared that frogs might exhibit variations in trajectory formation and in the underlying motor pattern when feedback was intact. For instance, bf28 showed an initial wiping limb trajectory (up to target limb contact) that was produced by staggered joint motion (i.e., knee flexion followed by hip extension). In bf38, the wiping limb trajectory (up to target contact) was produced by a more synchronous pattern of knee flexion and hip extension. In addition to these minor variations with feedback intact, there also appeared to be differences in the effects of deafferentation. For example, frog bf38 showed a relatively smaller effect of deafferentation on the wiping limb trajectory than did bf28.

In the following sections, we quantify changes in the wiping limb trajectory and the motor pattern after deafferentation. We then examine if feedback related to the initial posture of the wiping limb regulates motor-pattern and trajectory features. Finally, we quantify the variations observed in wiping limb trajectory among frogs, relate this variation to motor-pattern variations, and then examine if such variation can account for a frog’s susceptibility to deafferentation.

Effects of deafferentation on end-point trajectory

Because we observed variations among individual frogs in motor-pattern details and ankle path kinematics, we tested the statistics of a population of nine frogs in detail. We examined their data both as a group using lumped statistical measures and individually from different spatial positions. Figure 3A shows the unconstrained ankle paths of the wiping limb from different initial positions spanning the work space for a typical frog both before
and after deafferentation. Ankle paths are shown from movement onset up to target limb contact. After deafferentation of the wiping limb, the ankle paths demonstrate the qualitative kinematic features noted in the preceding text, namely an altered initial trajectory direction, decreased path straightness, and an increased maximal overshoot. Furthermore, Fig. 3 shows that there may be systematic differences in the magnitude of the change in path straightness and the initial trajectory direction based on the initial limb position. For example note that the paths starting from the more caudally extended positions of the frog stick figure are closer to the intact path than are the paths from the more rostrally originating positions (where the hip initially is flexed and the knee extended).

We calculated the combined, mean values of several kinematic variables for the nine frogs regardless of the initial position from which the wiping limb started. The normalized ankle path, the initial direction of the ankle trajectory relative to the hip, and the maximal overshoot were determined for all wipes for each frog. There were significant changes in each of these parameters following deafferentation. First, the combined, mean normalized path length (see calculation of path length in Fig. 1; 1.06 ± 0.06; mean ± SE) became significantly increased after deafferentation (1.25 ±0.10, significance $P < 0.01$). Second, our measure of the initial trajectory direction was altered after deafferentation. For this measure, we used the angle between the vector from the hip to the initial position of

![Figure 2](http://jn.physiology.org/Downloadedfromhttp://jn.physiology.org/)

**FIG. 2.** Digitized records and the corresponding raw EMGs during the hindlimb-to-hindlimb wiping reflex are shown for 2 frogs. Records are shown both before (A–D) and after (E–H) complete deafferentation of the wiping limb. Bold stick figures represent the wiping limb up to target limb contact. A bold line also traces the ankle path of both limbs (arrows mark direction of movement along the path), and a circled asterisk marks the point and frame of limb contact. A and C: with feedback intact, the kinematics of the wiping limb up to target limb contact was characterized by hip extension and knee flexion. During this initial phase, frog bf38 had a more synchronous pattern of knee flexion and hip extension, whereas bf28 had a more staggered pattern of knee flexion followed by hip extension. In both, knee extension followed limb contact in an attempt to remove the electrical stimulus. B and D: intact motor pattern was characterized by 3 periods of activity, separated here by vertical lines. Movement onset and contact (*) are indicated by the vertical arrows. Periods of activity consisted of an initial period of mainly BI, ventral head of semitendinosus (ST), and sartorius (SA) activity, a 2nd period of combined RI, semimembranosus (SM), BI, ST, and SA activity, and final period of vastus externus (VE) activity. Frog bf28 had a more distinct initial period. E and G: after deafferentation of the wiping limb, hip extension occurred earlier, faster, and to a larger extent in both frogs, and knee flexion was slowed, reduced, and even reversed to extension in mid-trajectory. This altered the initial ankle path (compare G and C). This resulted in the ankle overshothing and missing the stimulus initially. F and H: deafferented motor pattern was characterized by the reduced initial activity of BI, ST, and SA, an increased and broadened activity of RI and SM during the second period of activity, and the loss of knee extensor activity at limb contact.
FIG. 3. Frogs exhibit configuration-dependent kinematic deficits after deafferentation. A: ankle paths of the wiping limb from a number of different work-space positions are shown for frog bf11 both before (top) and after deafferentation (bottom) of the wiping limb. Only the paths up to target limb contact are shown. With feedback intact, the ankle paths were fairly straight from each position and ended at a similar location of contact with the target limb. After deafferentation, the initial direction of the ankle paths deviated caudally, and the paths became less straight and overshoot the normal location of limb contact. Ankle paths that started from work-space boundaries or rostral positions in the work space appeared to have larger path changes. B: ankle paths from individual locations exhibited low variability at each tested position in the limb’s work space. Paths are shown from 3 representative starting positions (1, 2, and 3) and up to target limb contact for both afferented (top) and deafferented (bottom) trials for frog bf25. Multiple trials were evoked at each. Ankle paths starting from position 2 exhibited the largest changes in curvature. C: averaged knee angle (left) and hip angle (right) changes that occurred in the wiping limb up to target limb contact are shown for frog bf25. Joint angle changes are shown for each of the 3 starting positions shown in B and for the same frog (see Fig. 1 for measurement of joint angles). After deafferentation of the wiping limb, there were early, middle, and late trajectory changes in the joint angle patterns. Early changes included an increased ratio of hip extension to knee flexion. Midtrajectory changes included the appearance of knee reversals, particularly at position 2. Late changes included an increased knee angle (less knee flexion) and an increased hip angle (increased extension) at the time of target limb contact.

the ankle and a vector characterizing the average initial direction of the ankle trajectory (see Fig. 1, b, for calculation). The combined, mean angle increased from $38 \pm 1.38^\circ$ to $66 \pm 1.7^\circ$, $P < 0.01$. Third, the maximal overshoot of the ankle path, also relative to the hip, was increased after deafferentation from a combined, mean of $39.5 \pm 2.13$ to $64.2 \pm 1.27$ (significant at $P < 0.01$). The values of the overshoot are in arbitrary pixel units but are normalized to the length of the frog’s limb to allow comparisons among frogs. The frog calf would be ~60 units in the normalized data. Finally, the peak tangential velocity of the ankle during the unconstrained wiping trajectory was increased after deafferentation from $416.75 \pm 1.5$ to $483.34 \pm 1.3$ units/s, $P < 0.01$. These values of end-point tangential velocity are again normalized to the length of the frog’s limb.

Consistency of kinematic changes after deafferentation across the limb’s work space

To more closely examine intertrial variability in end-point kinematics within an individual frog, we chose three test positions and elicited 10–12 wiping trials at each position before and after deafferentation. The three test positions chosen were similar among the 10 frogs tested. Each position required a particular pattern of joint motion to reach the target. These positions included (see Fig. 1): position 1 (knee extended at $120^\circ$, hip extended at $130^\circ$), position 2 (knee extended at $120^\circ$, hip flexed at $80^\circ$), and position 3 (the normal resting posture of the hindlimb; knee and hip both slightly flexed $80$ and $105^\circ$, respectively). Positions 1 and 2 required a larger flexion at the knee to reach the target region, caudal to the cloaca, where the stimulus is removed. In addition, position 2 required a larger hip extension relative to the other two positions to reach the same target region.

Figure 3B shows ankle path data (from movement onset up to target limb contact) at the three chosen locations. Our data demonstrated that multiple trials from a single location showed great consistency. Further, just as for the data described in the preceding text, there were systematic changes that occurred after deafferentation. The ankle path of the wiping limb was increased in length or became more curved. The initial trajectory direction was altered and caudally rotated, and the path overshoot was increased. In addition, as suggested in Fig. 3A, the magnitude of the change in both path straightness and the initial trajectory direction showed a position dependency (quantified for the group in Table 1). The normalized path length increased the largest at position 2, then 1, and the smallest at position 3. The largest changes in the initial trajectory direction were at positions 1 and 2. This suggested that changes in the initial trajectory direction were largest when the knee was initially in an extended configuration. Finally, the peak tangential velocity of the ankle trajectory was on average increased at each location after deafferentation (Table 1). How-
ever, the increase in velocity was largest for deafferented wipes starting from position 2 where the limb was both extended and rostral and key hip extensor muscles were most stretched (see DISCUSSION).

Effects of deafferentation on joint kinematics

Figure 3C shows the joint angle kinematics (hip and knee) obtained for the frog shown in 3B. We quantified three features of the joint angle data (Table 1): ratio of hip-to-knee movement during the first 85 ms of movement, peaks of hip and knee velocity, and hip- and knee-joint angles at the time of maximum overshoot. The joint angle plots in Fig. 3C show that after deafferentation, the early part of the wiping trajectory (1st 5 frames; 85 ms) was characterized by an increased hip extension and a decreased knee flexion from each position. This is the joint-based equivalent of the external rotation of the initial ankle trajectory, as described in the preceding text. The combined, mean ratio of hip extension to knee flexion after deafferentation has the largest percentage increase at position 1 and position 2; this accounts for the larger changes in the initial trajectory direction at these positions.

In addition to the early joint angle changes, we examined joint velocity profiles for the entire trajectory up to target limb contact. The hip- and knee-joint velocity profiles changed after deafferentation. Figure 4 shows the hip and knee velocities of the wiping limb for two frogs for wipes starting from position 2. Position 2 was unique in that all frogs (n = 10) displayed a prominent knee velocity reversal (from flexion to extension) after deafferentation of the wiping limb, which was absent in the afferented condition. The mean peak hip velocity was shifted relative to movement onset and was increased the most at position 2. This change in the hip velocity profile may be causally related to the appearance of the knee reversals (e.g., via an increase in interaction torques at the knee).

As mentioned in the preceding text, the overshoot of the ankle path relative to the hip was increased after deafferentation. An increased hip extension angle and a reduced knee flexion angle characterized the posture of the limb at the time of maximum overshoot (Table 1b). With the knee more extended during approach of the target limb, contact or collision with the target limb did not occur (i.e., was missed). Thus the hip continued extending until contact was made. In fact, for the group of frogs, the mean hip angle at maximum overshoot had a smaller variance after deafferentation than with feedback intact. This suggests that the hip joint limit might have been approached during deafferented trajectories. In addition to the decrease in knee flexion magnitude that contributed to the

![Averaged hip- and knee-joint velocity profiles](http://jn.physiology.org/)

**FIG. 4.** Averaged hip- and knee-joint velocity profiles (for 8 trials) are shown for wipes starting from position 2 for frogs b26 and b25: dotted lines, deafferented hip and knee velocity traces; solid lines, afferented hip and knee velocity traces. Top: knee velocities; Bottom: hip velocities. With feedback intact, there is some staggering between the peak knee and hip velocities (thin lines). After deafferentation, the hip begins to extend earlier, and in frog b25, hip extension is much faster (dotted lines). In addition, the knee begins to flex more slowly, reverses to extension in synchonony with the hip velocity profile, and finally reverses back to knee flexion (solid line). Position 2 was unique in that all deafferented frogs (n = 10) showed this knee velocity reversal. In addition, the normalized path length and peak hip velocity showed the largest increase for wipes starting at position 2 compared with the other 2 positions.
target overshoot, other factors may contribute including the increased hip velocity, end-point velocity, and presumably the lack of decelerative or dissipative muscle action. In contrast to the deafferented pattern, we observed that with feedback intact, the trajectory of the wiping limb in most frogs began to decelerate well before contact was made with the target limb. The limb contact or collision in the afferented frog is thus a controlled collision and is not the major source of deceleration when feedback was intact.

**Effects of deafferentation across the work space of the limb**

Figure 3, *A* and *B*, and the preceding analysis showed that changes in the ankle path after deafferentation, and in particular path straightness and initial trajectory direction, showed positional dependencies. To better quantify kinematic changes across the reachable work-space of the limb, we examined variations in normalized path length and initial trajectory direction from a larger range of initial limb positions (10–12 different positions as shown in 3A). We plotted how the mean change in each of these two parameters varied at initial positions spanning the work-space of the limb. Figure 5, *B* and *C*, shows contour plots of the mean change in the path straightness and the initial trajectory direction over the hindlimb work space. The coordinates for the contour plot are the initial work-space location of the ankle in polar coordinates (see 5A). The abscissa is the normalized distance of the vector from the hip to the ankle. The ordinate is the normalized angle between this vector and the mediolateral axis. The contours are the mean magnitude of change in the path straightness or in the initial trajectory direction. The lightest shading between contours represent the regions of largest change. The largest change in path straightness occurred when the ankle was positioned rostrally and distally relative to the hip (i.e., when the hip was flexed and/or the knee was extended). The largest changes in the initial direction were largely confined to regions where the knee was extended.

To demonstrate that the spatial variations observed in these

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**FIG. 5.** Position-dependent changes in wiping kinematics after deafferentation. *A*: wiping limb’s work space was divided into rings and sectors (see METHODS), and the average normalized path length and initial trajectory direction for ankle paths starting from each region were found before and after deafferentation for the group of 9 frogs. *B*: a gray shaded contour plot of the averaged change in the initial trajectory angle across the polar work space of the wiping limb. White coloring marks region of greatest change, black is least change. Largest changes in the initial trajectory angle were localized to regions of the work space where the limb is extended (radial distance >0.8). *C*: a contour plot of the averaged change in the normalized path length. Largest changes are localized to rostral regions (angle <0.4) where the hip is flexed (i.e., azimuth is small) and regions where the limb is extended (radial distance high). *D*: initial trajectory angle for the ankle path was changed after deafferentation from each region (0 indicates no change). Changes in the 2 sectors were roughly equal. Initial angle was significantly greater in the distal region where the knee is extended compared with the proximal region (*P* < 0.01). Vertical bars represent ±SD. *E*: normalized path length was changed in each region. Rostral sector where the hip is flexed had significantly larger changes than the caudal sector (*P* < 0.01), and the distal ring had larger changes than the proximal ring (*P* < 0.05) [**P* < 0.01, *P* < 0.05]. *F*: Cartesian coordinates of the initial ankle position were transformed into polar coordinates for the work space size of each frog. At each polar coordinate (open square and filled circle for instance), the value of the change in the normalized path length and initial trajectory direction was plotted. A contour plot was produced for each frog by interpolating over the sampled polar work space. Nine individual contour plots then were averaged for this figure.
data represented a significant trend in all tested frogs \((n = 9)\), we looked statistically at the positional dependency of changes in the path straightness and the initial direction. We divided the work space into discrete regions as in Fig. 5D. Each region comprised a sector or a segment of one of a set of concentric rings. Sectors could be classified as rostral or caudal relative to the hip. Rings could be classified as proximal or distal relative to the hip. In each region, we calculated the mean, combined change in both kinematic parameters. Figure 5, E and F, show that there was a positional dependency in the magnitude of change in both the initial trajectory direction and the path straightness after deafferentation. For instance, the path straightness was prone to larger changes when the ankle was initially positioned in the rostral versus the caudal sector \((P < 0.01)\) and in the distal versus the proximal ring segment \((P < 0.05)\). The initial direction was prone to larger changes when the ankle was positioned in the distal ring segments versus the proximal ring segments \((P < 0.01)\). The regions can be associated roughly with certain initial postures of the limb. For instance, in the rostral sector, the hip is mostly flexed while in the caudal sector, the hip is mostly extended. In the proximal ring the knee is mostly flexed, and in the distal ring, the knee is mostly extended. Thus postural-related feedback appears to play a significant role in regulating limb trajectories.

**Position-dependent motor-pattern adjustments**

We examined the motor patterns during wiping to quantify the extent of adjustment of motor pattern based on initial limb position. We examined these at the three test locations shown in Fig. 3B. For the muscles examined here, during wiping through the whisk phase, three periods of EMG activity could be discerned. These periods included: an initial period of limb flexor activity, a second period where hip extensors become additionally activated, and a final period of knee extensor activity that closely follows target limb contact. The first two periods of muscle activity contribute to the wiping limb trajectory up to target limb contact.

For the following set of data, raw EMGs for individual trials as shown in Fig. 2 were rectified and filtered. EMGs for multiple trials at the same position were aligned individually on the peak of the RI EMG envelope and then averaged together. We aligned EMGs in individual trials on the RI peak because of its ease of detection and its almost constant timing relative to stimulus onset between positions. This timing of the RI peak showed no significant differences between positions for individual frogs (Table 2). We analyzed, and present, only the data from frogs in which deafferentation abolished EMG variation and which therefore were free of artifact (e.g., Fig. 6C).

In Fig. 6A, averaged EMGs for six hindlimb muscles of the wiping limb for wipes starting at positions 1, 2 and 3 are shown for a frog whose kinematic data are presented in Fig. 3, B and C. The averaged EMGs in Fig. 6A show motor features that were consistent within the group of 10 tested frogs. To combine data for a group analysis and reduce trial to trial variations, EMGs for individual frogs were normalized based on the magnitude of their averaged EMG envelope at position 3. Thus after normalization all muscles had an envelope of unity at position 3. Position 3 was close to the normal, resting posture of the hindlimb in our experiments. Normalized data from individual trials were then averaged at each position. The data shown in Fig. 6A were subject to this normalization. Combining the data in this way revealed small but consistent and significant changes in EMG between each of the positions during the targeted portion of the wipe, which are presented in detail in Tables 2 and 3.

There were consistent changes between the three limb positions in the magnitude of the EMG envelopes of two groups of muscles. The first group of muscles include BI, SA, and ST, which are all muscles that contribute to knee flexion. The combined EMG data for the 10 frogs show a significant increase \((P < 0.01)\) of the normalized envelopes of BI and SA up to target limb contact at positions 1 and 2 compared with position 3 (see Table 3). In Fig. 6A, the averaged BI EMG at positions 1 and 2 was increased relative to the averaged EMG at position 3. In the figure, the first vertical line marks the averaged onset of limb movement and the second line marks the averaged time of target limb contact. Some of the increase in BI and SA, especially at position 1, actually occurred before the onset of limb movement in the horizontal plane. In fact, the combined EMG data showed significant increases in the magnitude of the averaged envelopes of BI and SA when these were calculated from the first detectable EMG up to movement onset (Table 3). ST, another knee flexor that would be lengthened concomitantly at positions 1 and 2, showed no significant differences in the magnitude of the averaged envelope up to movement onset. However, the averaged ST envelope in the later period up to target limb contact was increased at these positions relative to position 3 (Fig. 6A).

There were also consistent changes between the three limb positions in a second group of muscles, the hip extensors RI, SM, and AD. However, although significant, these changes were small and therefore are not shown graphically. In the wipe type discussed here, this second muscle group was involved in the free-limb motion. This group of muscles also contributed to the postcontact interaction phase, and the early part of the whisking phase that serves to remove an irritant from the target limb. In this group, variation occurred in the timing of the onset of the strong hindlimb muscles RI, SM, and AD relative to the onset of BI. It is important to emphasize that the peak timing of these muscles did not vary. There was no difference between the onset of BI and the peak EMG of RI or SM between positions. However, the onset of RI and SM relative to the onset of BI changed between positions \((P < 0.05)\). In the combined data, the latency was shortest at position 3, then position 2, and longest at position 1 (see Table 2). The latency differences appeared to be due primarily to the broadening of the rising phase of the EMG envelopes of RI and SM.

### Table 2. Mean values of EMG timing parameters

<table>
<thead>
<tr>
<th>EMG Data</th>
<th>Stim Onset to RI Peak</th>
<th>BI Onset to RI Onset</th>
<th>BI Onset to RI Peak</th>
<th>RI Duration</th>
</tr>
</thead>
<tbody>
<tr>
<td>Position 1</td>
<td>940 ± 7</td>
<td>383 ± 20**</td>
<td>636 ± 22</td>
<td>413 ± 20**</td>
</tr>
<tr>
<td>Position 2</td>
<td>950 ± 8</td>
<td>302 ± 20**</td>
<td>611 ± 21</td>
<td>499 ± 20</td>
</tr>
<tr>
<td>Position 3</td>
<td>939 ± 8</td>
<td>283 ± 19</td>
<td>602 ± 22</td>
<td>518 ± 20</td>
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<tr>
<td>Deaf-position 1</td>
<td>928 ± 7</td>
<td>207 ± 12**</td>
<td>536 ± 15**</td>
<td>689 ± 17**</td>
</tr>
<tr>
<td>Deaf-position 2</td>
<td>935 ± 7</td>
<td>220 ± 13**</td>
<td>529 ± 15**</td>
<td>672 ± 18**</td>
</tr>
<tr>
<td>Deaf-position 3</td>
<td>941 ± 7</td>
<td>211 ± 12**</td>
<td>522 ± 15**</td>
<td>679 ± 18**</td>
</tr>
</tbody>
</table>

Values are means ± SE. ** Significantly different at \(P < 0.01\) from values at position 3 with feedback intact.
rather than phase shifting of the peaks. Changes in EMG duration of RI and SM were related inversely to the latency changes, whereas envelope termination times were similar across positions in these muscles. These data suggest a role of (presumably proprioceptive) afferents, in regulating or gating the onset of this muscle group. The combined data for the 10 frogs demonstrate these trends clearly (Table 2).

A final and third muscle group becomes activated near the end of the RI/SM/AD EMG envelopes and is involved in the subsequent kinematic phase of whisk/extension. These are the knee extensors (represented by VE here). VE showed no consistent regulation of EMG activity based on the initial limb position.

To summarize, there were changes in the magnitude and timing of specific EMG envelopes based on the initial limb posture. The changes in magnitude were restricted primarily to an initially activated group of relatively smaller muscles that act to flex the knee. Changes in onset timing occurred in a
group of relatively large muscles that extend the hip, but the timing of their peak and termination was unaffected. It was unexpected to us that these muscles would be delayed in the onset of their activation without other phase shifts throughout the motor pattern.

Changes in motor pattern after deafferentation

After deafferentation of the wiping limb, there were several changes in the motor patterns. These changes contribute to the altered free-limb kinematics of the placing phase of the hindlimb wipe after deafferentation. Figure 6B shows the averaged EMG envelopes for hindlimb wipes starting from position 1 before and after deafferentation of the wiping limb. Once again the plots are aligned on the peak of the RI EMG envelope. In the frog shown, deafferentation resulted in a reduced latency between the onset of BI EMG activity and the activity of a second group of muscles (RI, SM, AD mainly). The reduced latency between BI onset and RI/SM/AD onset was due to the reduction of initial BI EMG strength and concomitant delayed onset of RI and the broadening of RI and SM EMGs. In addition to this altered onset timing, the peak EMG activity of RI, SM, and AD often was increased, as is the case for \textit{b}25. Finally, there was a conspicuous absence of VE activity that normally closely follows limb contact. This loss correlates with the loss of the kinematic extension phase (not shown) after deafferentation (see Fig. 2).

We computed the integrated values of the precontact hindlimb EMG envelopes for the 10 frogs before and after deafferentation at each position. We thus focused only on the envelopes up to limb contact (those contributing to the placing phase kinematics). The mean duration of this phase of movement was similar before and after deafferentation so that any magnitude changes are not related to computing the integrated EMG values over longer or shorter movement durations. Examples of the data are in Table 3. Our first observation was that the mean, integrated BI EMG at positions 1 and 2 is reduced significantly \((P < 0.01)\) after deafferentation. The EMG of SA is reduced significantly at position 1 as well. Second, the mean, integrated EMG of particular muscles of the second group (RI, SM, and AD) is increased significantly during the wiping kinematics up to limb contact \((P < 0.01)\). The increased magnitude is attributable to two factors. First, the EMG envelopes of these muscles broadened to overlap more with the initial BI, SA, and ST EMGs: the combined, mean durations of RI and SM increased by 18 and 15%, respectively, at each position. Second, the peak EMG was advanced relative to BI onset: the mean latency between the onset of BI EMG and the peak EMG of RI and SM was reduced by 45.5 and 40.2%, respectively. Because these changes in RI and SM occurred before limb contact, they must be attributed either to initial postural or later on-line afferent effects. We will show in the following text that these motor changes resulting from complete deafferentation are not present after cutaneous deafferentation alone.

To summarize, there are several changes in the wiping motor patterns that contribute to the altered kinematics of the wiping limb after deafferentation. First, the regulation of BI and SA EMG activity based on the initial position of the limb is absent. Therefore knee flexor related EMGs are not increased when these muscles initially are lengthened. Second, muscles of a second group that generate large hip extensor torques contribute more to the unconstrained wiping movement. Finally, in some frogs the initial BI or SA activity may collapse completely or disappear, leading to a single, synchronous activation pattern of most muscles. Thus the combined effect of these EMG alterations resulted in a deafferented motor pattern with less differentiated periods of activity (i.e., more synchronous knee flexor and hip extensor activity). Functionally, these changes led to increases in the amount of hip extensor activity up to target limb contact and to decreases in the amount of knee flexor/hip flexor activity that contribute to trajectory formation.

Afferent modality


cutaneous afferents. Changes in the motor pattern and kinematics after deafferentation were described in detail in the preceding text. The changes described thus far could be due to the absence of feedback from any one or several distinct afferent types from within the wiping limb. Further, it is also conceivable that some of the changes result from bilateral interactions of feedback or less specific effects such as the presence of asymmetric, contralateral phasic feedback from the moving target limb. In this section, we establish that the major kinematic and motor-pattern changes we remarked on in the preceding text were due mainly to the loss of ipsilateral muscular and joint afferents.

To test the relative importance of cutaneous and proprioceptive afferents, we selectively abolished input from cutaneous afferents alone. Figure 7A shows the ankle paths of the wiping limb starting from three locations in the work space. Wipes first were elicited with afferents intact (bold lines). Then after transecting ipsilateral cutaneous nerves, wipes were elicited at the same position (dotted line). The path of the ankle does not appear changed. In 4/4 frogs that received a complete cutaneous deafferentation of the wiping limb, the average work-space measure of path straightness did not change significantly (mean of 1.07 ± 0.04 with intact feedback to a mean of 1.06 ± 0.03

<table>
<thead>
<tr>
<th>EMG Data</th>
<th>RI</th>
<th>AD</th>
<th>SM</th>
<th>ST</th>
<th>BI</th>
<th>SA</th>
<th>ST (to onset)</th>
<th>BI (to onset)</th>
<th>SA (to onset)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Position 1</td>
<td>0.84 ± 0.14</td>
<td>0.83 ± 0.16</td>
<td>0.95 ± 0.08</td>
<td>1.07 ± 0.04</td>
<td>1.28 ± 0.07**</td>
<td>1.65 ± 0.09**</td>
<td>1.02 ± 0.06</td>
<td>1.30 ± 0.06**</td>
<td>1.70 ± 0.12**</td>
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<tr>
<td>Position 2</td>
<td>1.05 ± 0.12</td>
<td>0.91 ± 0.15</td>
<td>1.06 ± 0.08</td>
<td>1.13 ± 0.07*</td>
<td>1.15 ± 0.04**</td>
<td>1.47 ± 0.12**</td>
<td>0.98 ± 0.07</td>
<td>1.12 ± 0.04*</td>
<td>1.10 ± 0.14</td>
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<tr>
<td>Position 3</td>
<td>1.00 ± 0.13</td>
<td>1.00 ± 0.13</td>
<td>1.00 ± 0.07</td>
<td>1.00 ± 0.06</td>
<td>1.00 ± 0.05</td>
<td>1.00 ± 0.10</td>
<td>1.00 ± 0.07</td>
<td>1.00 ± 0.06</td>
<td>1.00 ± 0.10</td>
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<tr>
<td>Deaf-position 1</td>
<td>1.42 ± 0.24**</td>
<td>2.14 ± 0.15**</td>
<td>1.80 ± 0.49**</td>
<td>0.92 ± 0.09</td>
<td>0.84 ± 0.12*</td>
<td>1.11 ± 0.20</td>
<td>0.92 ± 0.09</td>
<td>0.75 ± 0.12*</td>
<td>0.85 ± 0.12*</td>
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<tr>
<td>Deaf-position 2</td>
<td>1.50 ± 0.21**</td>
<td>1.95 ± 0.20**</td>
<td>1.88 ± 0.42**</td>
<td>0.95 ± 0.11</td>
<td>0.75 ± 0.15*</td>
<td>1.20 ± 0.15</td>
<td>0.95 ± 0.11</td>
<td>0.72 ± 0.15*</td>
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<tr>
<td>Deaf-position 3</td>
<td>1.48 ± 0.28**</td>
<td>2.02 ± 0.25**</td>
<td>1.77 ± 0.41**</td>
<td>0.89 ± 0.10</td>
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<td>1.17 ± 0.22</td>
<td>0.89 ± 0.10</td>
<td>0.73 ± 0.08*</td>
<td>0.79 ± 0.12*</td>
</tr>
</tbody>
</table>

Values are means ± SE. Each muscle normalized to average area of electromyographic (EMG) envelope at position 3 with feedback intact. RI, rectus internus; AD, adductor; SM, semimembranosus; ST, ventral head of semitendinosus; BI, biceps; SA, sartorius. ** Significantly different at \(P < 0.01\) from values at position 3 with feedback intact. * Significantly different at \(P < 0.05\) from values at position 3 with feedback intact.
after cutaneous deafferentation). In Fig. 7A, after ipsilateral dorsal rhizotomy of the same frogs, the initial direction, straightness, and overshoot of the ankle path (dashed lines) became altered in the manner described previously in this paper. The average work-space measure of the path straightness for the four frogs after dorsal rhizotomy was 1.30 ± 0.08.

The EMG envelopes in Fig. 7B are averages of eight wipes in each condition. After cutaneous deafferentation, the relative phasing between the initial knee flexor activity (represented by BI and ST) and hip extensor activity (represented by RI) was maintained, and the magnitude of the envelopes up to limb contact was similar (7B, top). This suggests that the reduced latency between the initial period of limb flexor activity and the second period of hip extensor activity, which occurred after deafferentation, might be caused by loss of proprioception. During the later portions of the wiping reflex (i.e., when the limbs were mechanically interacting with one another), our data showed in some frogs (3/5) a deletion of the VE period or irritant removal phase (not shown here). This suggests that cutaneous afferents may function to trigger this final phase of activity. After complete dorsal rhizotomy (of the previously cutaneously deafferented frog), the two major EMG changes, typical for a deafferented frog developed (7B, bottom). In particular, the hip extensor EMG’s envelopes were broadened and their peaks increased, and the initial EMG burst in BI was decreased. In summary, the trajectory up to target limb contact and the underlying motor pattern showed no significant difference as a result of cutaneous deafferentation in the tested frogs. However, there were kinematic and motor-pattern differences in later phases; this suggests an alternative role for cutaneous feedback (i.e., roles not related to regulating the trajectory up to limb contact).

**CONTRALATERAL DE-EFFERENTATION.** To examine the possibility that there was a reorganization or disruption of a normal centrally driven wiping motor program by contralateral phasic afference, due to the absence of balancing ipsilateral afference, we immobilized the target limb by ventral rhizotomy. After a series of wipes in five frogs with complete ipsilaterally deafferented hindlimbs, we transected the contralateral ventral roots in the frogs and positioned the target leg in the usual starting position. This manipulation allowed us to continue to stimulate the skin of the target limb while preventing limb motion and beta-fusimotor activation of muscle spindles. If asymmetric phasic feedback from the unaffected target limb contributed strongly to the kinematic and motor-pattern changes seen after deafferenting the wiping limb, we expected that the ventral rhizotomy would restore the normal pattern or would result in additional large alterations in motor-pattern structure.

Figure 7C shows the ankle paths of the wiping limb starting from three positions in the work space for frog bf19. The bold
lines represent the initial paths with afferents intact. After an initial ipsilateral dorsal rhizotomy, the initial direction, straightness, and overshoot of the wiping paths (dashed lines) were changed as described in the preceding text. After contralateral ventral root rhizotomy, the paths (dotted lines) did not return to normal. In the combined kinematic data for the five frogs, the mean value for the path straightness was initially 1.08 ± 0.05. After deafferentation, the mean increased to 1.24 ± 0.07, and after contralateral ventral rhizotomy the combined mean did not change significantly and was 1.20 ± 0.06. However, the peak tangential velocity of the limb decreased from 490 ± 8.2 to 450 ± 10.5 units/s. The decreased velocity of the limb is probably due to some reduction in R/SM peaks after the ventral rhizotomy (Fig. 7D).

The EMG correlates of the kinematic changes for frog bf19 are shown in Fig. 7D. The averaged EMG envelopes of BI and RI are shown for each condition. This particular frog has a wiping motor pattern without a distinct initial BI peak (7D, top). Nonetheless after deafferentation the increased peak and broadening of the RI and SM EMG envelopes resulted in a larger hip extensor contribution to trajectory formation. In addition there were some small changes in the initial BI EMG activity. After the ventral rhizotomy, the entire motor pattern became weaker. The EMG bursts of both BI and RI were narrowed and their peaks reduced (7D, bottom). For the combined data, the mean percentage decrease in the peak EMG of BI and RI was 8.5 and 9.2%, respectively for the five frogs after the ventral rhizotomy. It is possible these values could have been varied by moving the target leg (see e.g., Chepelyugina 1947; Giszter et al. 1989) but this possibility was not explored here. However, the normal motor pattern and balance of EMG activity was not restored. The general EMG reduction suggests that phasic contralateral afferent feedback might play a role in regulating the strength or excitability of the contralateral wiping pattern. Nonetheless the dominant cause of the kinematic and motor-pattern alterations reported here were due to the loss of feedback from the wiping limb and in particular proprioceptive feedback.

The results of the last two subsections suggest that the significant changes in limb kinematics were not due solely to the loss of cutaneous feedback or to the effects of asymmetric (or unbalanced) contralateral feedback. Instead it appears that tonic and phasic inputs from muscular and/or joint afferents of the wiping limb contribute to the selective excitation of muscles of the initial knee flexor group and to the selective inhibitory control of the hip extensor group of muscles.

**Relating kinematics and motor-pattern variations**

In previous sections, we presented the major qualitative kinematic and motor-pattern changes in the wiping limb after its deafferentation. In addition, we examined alterations in joint based motion and motor pattern more quantitatively. We showed consistent changes in both the wiping limb kinematics and motor pattern after loss of proprioception. However, as first reported for the frogs shown in Fig. 2, the effects of deafferentation varied somewhat among frogs. In this section, we examine such variations using our database of kinematic and motor-pattern data. We related kinematic variation to motor-pattern variation both before and after deafferentation.

**Variations of ankle path measures and deafferentation effects**

We first examined the distribution of changes in the normalized path lengths of the ankle after deafferentation in a total of 31 frogs. Figure 8A shows the individual ankle paths for the 31 frogs before (dark lines) and after (gray lines) deafferentation of the wiping limb. The paths for each frog begin from roughly similar positions in the work space with the initial hip and knee angles ~90 and 105°, respectively. The distribution of maximal changes in normalized path length ranged from 0.09 to 0.45 (shown in Fig. 8B), and the distribution was trimodal with respect to the degree of change. There was a group of six frogs that had little to no difference in path straightness (<0.09) after deafferentation. This value of 0.09 was not significantly different from the variation seen in a single frog on multiple trials. The other 26 frogs all had significant changes >0.09. These frogs comprised two subgroups. The large majority of frogs (16/31) fell into a first subgroup with changes in path straightness between 0.09 and 0.39. The rest of the frogs (9/31) were in a second subgroup with changes in path straightness >0.39.

**Motor pattern predicts kinematic effects of deafferentation**

Specific motor-pattern effects explained the structure of the distribution and the range of changes after deafferentation shown in Fig. 8, A and B.

In the first group of frogs in Fig. 8B (6/31), the path changes after deafferentation were minimal. In these frogs, we observed no configuration-based modulation of EMG activity in muscles comprising this initial flexor group even when full afference was intact (8C, frog bf35). After deafferentation, these same frogs also showed little change in the magnitude or phasing between SA, BI, and ST and the muscles of the hip extensor group (mainly RI, SM, AD). In such frogs, the motor pattern was largely synchronous when feedback was intact and muscle timing was maintained centrally rather than depending on affereents.

All frogs in the second group in Fig. 8B (exhibiting path changes between 0.09 and 0.33 after deafferentation) showed a reduction in the initial EMG activity of BI, SA, and ST. Seventy percent of these frogs exhibited this reduction without any increase in the magnitude or duration of RI, SM, and AD. This is exemplified by bf29 in Fig. 8C. Thirty percent of these frogs in this subgroup also showed relatively small increases in the magnitude of RI, SM, and AD EMGs.

Frogs exhibiting path changes <0.33 (i.e., the 3rd subgroup of 8B) always showed an increase in the magnitude and duration of RI, SM, and AD. This is exemplified by bf31 in 8C. In addition, most (8/9 or 88%) of these frogs also had a reduced magnitude of the initial BI, SA, and ST EMG, like the frogs in the second subgroup in 8B. This is shown for frog bf25 in Fig. 8C. The largest path changes after deafferentation therefore are related to the increased activation of the powerful hip extensors RI and SM during the unconstrained trajectory of the wiping limb. These same frogs had relatively large increases in the end-point velocity (or by inference kinetic energy of the limb). The additional loss of knee flexor related activity presumably contributes to the altered initial trajectory direction and/or reduced anticipatory control of interaction torques at the knee.
Thus the presence or absence of specific motor-pattern changes after deafferentation predicts the degree of variation of change in the ankle path length. Three main ankle path changes are seen, namely an altered initial trajectory direction, an increased path length, and an increased overshoot. However, the changes vary between frogs. The presence of changes in the normalized path length after deafferentation is shown for the group of 31 frogs. Distribution is trimodal with respect to the presence of visually detectable change (i.e., changes >0.09). Frogs that have changes >0.09 form 2 subgroups, those with changes >0.39 and those with moderate changes between 0.09 and 0.39. Each peak in the histogram shown in B was associated with ≥ 1 specific motor-pattern changes caused by deafferentation. Examples of these motor patterns and their changes are shown in 4 separate frogs (left to right). Rectified EMGs are shown for BI and ST, representing the knee flexor phase, and RI and SM, representing the hip extensor phase, both before and after deafferentation. Magnitude of each EMG, for ST, BI, RI, and SM, was normalized to the maximum amplitude of that muscle (either in the afferented or deafferented trial). Thus EMG amplitudes range from 0 to 1. Frogs in the first subgroup of the distribution shown in B were exemplified by bf35, which showed little change in a largely synchronous motor pattern (i.e., little difference in phasing between knee flexors and hip extensors; onset of knee flexors marked by vertical line and time of half-peak of hip extensors marked by 2nd vertical line). Frogs in the 2nd subgroup shown in B were exemplified by bf29, which showed longer latencies between knee flexor and hip extensor activation. After deafferentation, there was a specific reduction of the initial phase of knee flexor activity (marked by asterisk) and collapse into a more synchronous pattern similar to bf35. Frogs in the 3rd peak of B were exemplified by both bf25 and bf31, which both showed a prominent increase in hip extensor activity after deafferentation. bf25 also showed a reduction of an initial well-differentiated phase of knee flexor activity, similar to bf29.

**Variations of joint coordination and effects of deafferentation**

Using 10 frogs from the preceding group of 31, we examined variations in the joint coordination that might account for variations in the degree of change in the normalized ankle paths after deafferentation. We examined these from the three test positions (shown in Fig. 3B) and for many wiping movements. For these
frogs, digitization of the joint positions was performed for ≤30 wipes before and 30 wipes after deafferentation for each frog. We found that we could explain 72% ($r^2 = 0.72$) of the variation of the change in the normalized path length with the changes in two joint trajectory variables: the change in the peak hip velocity and the change in the initial ratio of hip extension to knee flexion (measured during the first 5 frames of movement, i.e., the joint path measure of the initial trajectory direction of the ankle). Both variables were significantly positively correlated to the change in the normalized path length (change in peak hip velocity at $P < 0.001$ and the change in the ratio of hip extension to knee flexion at $P < 0.05$). Frogs with larger changes in the normalized path length of the ankle after deafferentation tended to have larger increases in the ratio of hip extension to knee flexion at the initiation of wiping and larger increases in peak hip velocity around midtrajectory.

We then examined variations in joint coordination in our database of 31 frogs. Figure 9, A and B, shows the afferented and deafferented joint paths (i.e., the joint-based equivalents of the Cartesian ankle paths) for the 31 frogs shown in Fig. 8. The afferented joint paths showed a significant degree of variation between frogs in the patterns of knee and hip coordination. The coordination patterns of afferented frogs ranged from nearly complete joint staggering (knee flexion followed by hip extension) to more synchronous patterns. We therefore examined whether the pattern of joint coordination in afferented spinal frogs predicted a frog’s susceptibility to the effects of deafferentation.

We found that the degree of joint staggering in the afferented condition predicted the initial changes in the joint path after deafferentation. To measure the initial joint path change after deafferentation we calculated the area between the afferented

![Figure 9](http://jn.physiology.org/)

**FIG. 9.** Features of the afferented joint path and motor pattern predict the degree of change in the deafferented joint path. A: plot of proximal joint paths pre- and postdeafferentation for the 31 frogs are shown. Cartesian ankle paths (in Fig. 8) were transformed into joint coordinates (ordinate = hip angle, abscissa = knee angle). Black traces represent afferented paths, and gray traces represent deafferented paths. Afferented frogs show differences in the joint coordinate path that reflect variations of knee-hip-joint coordination during the placing phase. Differently colored frogs show changes in the joint coordinate trajectory during placing that reflect earlier and larger degrees of hip extension and reduced degrees of knee extension. Most of the deafferented frogs also display marked knee angle reversals around midtrajectory. B: only the first one-third of the afferented joint space path (initial joint path in C) shown in A is plotted. Averaged slope of this initial path varies in afferented frogs from 0, or nearly pure knee flexion, to slopes that indicate larger initial degrees of hip extension combined with knee flexion. Straight-line diagonal has a slope of $-1.0$ and marks the path the ankle would follow if equal rates and magnitudes of knee flexion and hip extension occurred at the onset of the placing phase. C: degree of change in the initial, deafferented joint coordinate path is related to the slope of the initial, afferented joint space path shown in B. Slope of the joint space path is a measure of the ratio of motion at hip and knee. Zero represents pure knee motion; $-1$ represents equal motions of hip and knee. Change and the afferented joint path slope are correlated significantly ($P < 0.02$), and the slope of the afferented joint path can account for 25% ($r^2 = 0.25$) of this measure of the change in the joint path after deafferentation. Frogs with more asynchronous and equal rates of knee flexion and hip extension (afferented slopes closer to $-1$) at the onset of placing tended to show smaller changes in their pattern of coordination after deafferentation. D: latency between the onset of BI, a knee flexor, and the time to half-peak of RI, a hip extensor, was a significant determinant of the initial slope of the joint path ($P < 0.01$) and accounted for 48% of the variability of the initial afferented slope. Frogs with increased separation between the 2 muscle groups (knee flexor and hip extensor related) had smaller slopes. These frogs also showed increased susceptibility to change after deafferentation.
and deafferented joint paths for each frog over the first third of the trajectory. We related this measure to the hip/knee-joint movement ratio when feedback was intact. A scatterplot of the two variables is shown in Fig. 9C. The ratio of hip-to-knee movement over the first third of the trajectory was correlated negatively (significant at $P < 0.05$) to the change observed in the initial portion of the deafferented joint path. Afferented frogs with larger initial ratios of knee flexion to hip extension tended to show larger changes in the initial portions of the wiping trajectory after deafferentation. The range of initial hip and knee ratios in afferented frogs collapsed to a more uniform joint coupling ratio in the deafferented condition. The relatively low $r^2$ value of 0.35 indicates that this is only one contributing component and predictor of changes after deafferentation.

We examined accuracy of the motion to target and combined this with our measures of ankle path straightness. We found that afferented frogs with longer normalized Cartesian path length (i.e., higher ankle path curvature and more synchronous joint motion) were less likely to show effects of deafferentation by overshooting and missing the target (Table 2).

Taken together, these observations suggested to us that frogs that exhibited more curved Cartesian paths and more synchronous joint coordination at the outset showed less coordination change after deafferentation. We inferred that such frogs did not make strong use of proprioception in wiping (e.g., peak 1 in Fig. 8B). Frogs that generated trajectories with straighter end-point paths at the outset, by phase staggered joint use, were more affected by loss of proprioception. We infer such frogs implemented trajectory controls that made strong use of proprioception to determine motor-pattern phasing and amplitude.

Relating kinematics and motor pattern quantitatively

We found that, when their afferents were intact, frogs with low initial hip-to-knee-joint ratios in the initial motion (i.e., joint staggering) also had increased latencies between the onset of BI and the time to half-peak of RI compared with other frogs. A scatterplot of the two variables is shown in Fig. 9D. The two were correlated significantly at $P < 0.01$ with $r^2 = 0.48$. Thus the longer the latency between BI and RI for an individual frog and therefore the more the motor pattern consisted of two separately phased muscle groups, the more staggered the joint path of the placing phase was. These frogs, as mentioned in the preceding text, tended to have larger changes in the initial portion of the joint space path after deafferentation. After deafferentation, the latency between BI onset and RI half-peak was reduced, and the degree of the reduction in latency was correlated positively to the degree of change in the initial joint-coordination path ($P < 0.01$). The magnitude of the latency reduction accounted for 48% of the variability in the change of the joint-coordination path after deafferentation.

In the preceding section, we showed that 72% of the changes in end-point kinematics after deafferentation could be explained by the combination of change in hip-to-knee-movement ratios and change in peak hip velocity. After these analyses, we could predict the degree of change in the initial trajectory direction after deafferentation based on the relative latency of biceps and rectus internus onsets. This latency related to the initial hip/knee movement ratio. Further, the other factor in end-point kinematic changes, namely the change in peak hip velocity, is accounted for by the increased magnitude of RI and SM EMGs, the hip extensor group, after deafferentation.

Discussion

This paper has demonstrated clear changes in both the wiping limb kinematics and the underlying motor pattern after deafferentation in spinal frogs. Our data can be related to several areas in spinal motor control: trajectory or path planning by spinal mechanisms, multijoint muscle control, modularity of spinal systems, and uses of feedback in trajectory control. These relationships are examined briefly in the following text, preceding a broader discussion of the data themselves.

Trajectory formation in the spinal cord

Our data relate directly to trajectory formation by the spinal cord and the role of feedback in trajectory formation. In the form of wiping studied here, the ankle represented the limb effector and therefore the end point to be controlled and positioned at the site of the irritant. After deafferentation, ankle trajectories had an increased velocity, an altered initial direction, and an increased path curvature during the targeted portion of wiping. The extent of these effects varied among frogs and was related somewhat to trajectory organization when feedback was intact. Frogs with more synchronous hip- and knee-joint motion usually showed smaller effects of deafferentation. Frogs with more staggered joint motion (knee flexion then hip extension) showed larger changes in ankle path length after deafferentation. These different susceptibilities among frogs were already visible at movement onset as differences in the initial trajectory direction. It is also worth remarking, however, that hip velocity increased after deafferentation, and interaction torques that would presumably act to extend the knee also will have increased (e.g., Hollerbach and Flash 1982). The knee velocity reversals that we frequently observed thus may represent the effects of increased interaction torques. These reversals led to dramatic curvatures in the ankle path of some frogs after deafferentation. Proprioceptive roles in the coordination of adjacent joints during reaching trajectories have been shown in man (Sainburg et al. 1995). Here we have shown that aspects of such a strategy may be organized spinal. In our data, different frog spinal cords may have embodied (or acutely exhibit) the joint staggered strategy for trajectory formation and its proprioceptive control to differing degrees.

Multijoint controls

Feedback control of muscle properties is likely to be a significant factor in our data, although not addressed directly. When the ankle was positioned in work-space boundaries (i.e., with extended knee angles), frogs showed the largest change in initial trajectory direction after deafferentation. The position-dependent deviation in the initial acceleration of the ankle was consistent with deafferentation causing loss of active compensations. These are likely to include compensation for muscle length (Nichols and Houk 1976), for moment arm (Nichols et al. 1998), and perhaps for configuration-based variation of the inertia tensor of the limb. In human trajectories, compensations for the inertial anisotropy of the limb are included in path planning (Sabes et al. 1998) and may be derived propriocep-
tively (Ghez and Sainburg 1994). The presence of deviations in the wiping trajectory at movement onset is consistent with the importance of postural feedback in the initial set up of the ensuing motor pattern or in the regulation of motor neuron excitability. It is presently unclear if the position-related feedback is due to tonic feedback (i.e., the population of resting muscle spindle discharges), to phasic feedback (e.g., muscle spindle bursts due to beta-fusimotor activation) at motor-pattern initiation, or to both.

**Body scheme and modularity**

Our data could be interpreted in terms of spinal body scheme information and internal models as has been suggested previously in frog wiping behaviors (Berkinblitt et al. 1986; Fukson et al. 1980). For example, feedback in early phases might serve to set up the execution of the ensuing trajectory. This would be consistent with parameterizing an internal model of limb dynamics and the environment (e.g., Buneo et al. 1995; Flanagan and Wing 1997; Gandolfo et al. 1996; Ghilardi et al. 1995; Gurfinkel et al. 1982; Imamizu et al. 1998; Lacquaniti et al. 1992; Shadmehr and Mussa-Ivaldi 1994; Vicario and Ghez 1984; Wolpert et al. 1995). In this case, the model would be resident in the spinal cord. Such a model might be either explicit or implicit and might be a general limb trajectory model or might be very specific to the wiping reflex. Only much more extensive experimentation could address these issues.

The data we have presented also can be related to an analysis of the wipe as composed of motor primitives (Bizzi et al. 1991, 1995; Giszter et al. 1993a), and the results could be taken to represent significant modulation of one or more primitives by proprioeptive feedback. When feedback was intact, some muscles tended to covary strongly between initial limb positions during wiping (e.g., BI and SA and RI, SM and AD). In addition, deafferentation produced common motor-pattern changes in these component muscle groups, e.g., RI, SM, and AD (hip extensor phase of wiping) tended to have broadened and increased peaks of activation and BI and SA (initial knee flexor phase) tended to have reduced initial EMG bursts. These EMG groupings might represent biomechanical primitives. This will be explored further in following papers.

**Deafferentation and afferent modality**

The primary effects observed in this study were due mainly to the loss of proprioeceptive feedback. Cutaneous deafferentation of the wiping limb produced no detectable change in the motor pattern and kinematics during the targeted portion of wiping. However, there were some changes in EMG activity after target limb contact after cutaneous deafferentation. In particular, the absence of VE activity that normally closely follows limb contact suggests that feedback from cutaneous receptors may play a role in triggering VE (knee extensor) activity and the whisking phase (Giszter et al. 1989). Cutaneous feedback also has been shown to play a critical role in obstacle detection during the targeted portion of wiping (before limb contact) and serves to trigger correction responses that circumvent path obstacles (Kargo and Giszter 2000).

The procedure of cutting the contralateral ventral roots was used to eliminate asymmetric phasic feedback due to motion and to beta-fusimotor modulation of spindle intrafusal fibers from the target limb. Muscle spindles have clear contralateral effects including influences on motoneurons, reflex strength, primary afferent depolarization, and motor-pattern phasing in mammals (Appelberg et al. 1984; Brooke et al. 1997; Grillner and Rossignol 1978a,b; Hiebert et al. 1996; Jankowska et al. 1978), and effects on reaching in man (Lackner 1984). Tendon organs also may have significant contralateral effects (Lafluer et al. 1993). After deafferentation of the wiping limb and de-efferentation of the target limb, wiping proceeded in an essentially feedforward manner, equivalent to a fictive preparation. De-efferentation did not restore the normal kinematics or motor pattern in the previously deafferented frog. Thus asymmetric phasic feedback to a bilaterally distributed or bilaterally influenced core of interneurons (e.g., see Stein et al. 1995; Ting et al. 1998) was not the major source of kinematic and motor-pattern change observed after deafferentation. Despite this, contralateral feedback may have importance during the normal wiping behavior as detailed in the preceding text (e.g., adjusting reflex gains and motor-pattern phasing). The modest reduction in activation levels of the entire motor pattern after de-efferentation suggests that at the least contralateral feedback regulates the general excitability and strength of the wipe. Feedback from the contralateral limb also has been demonstrated to interrupt and inhibit wiping in frogs (Chepelyugina 1947; Giszter et al. 1989) and to modulate or switch the spinal frog’s choice between flexion withdrawal and wiping in responding to the same noxious stimulus (Schotland and Giszter 1993).

**Roles of proprioceptive afferents in wiping trajectory control**

The possible roles of proprioceptive feedback from ipsilateral afferents in regulating wiping trajectories are several-fold. We cannot currently discount the possibility of a sizeable role of joint afferents in our data (see e.g., Amassian et al. 1998). In evaluating muscle afferent contributions, we considered that feedback could provide nonspecific excitation or inhibition to the spinal cord circuitry underlying wiping; act to regulate individual muscle properties in isolation (homonymous feedback) (Nichols and Houk 1976), or as a group (heteronymous effects) (e.g., Bonasera and Nichols 1994); establish a background level of excitation of motor pools, which therefore determines their recruitment thresholds, initial firing rates, and details of muscle onset times (Gribble et al. 1997); be used as a set of gates, triggers, or delays to organize the detailed timing of a motor program or pattern generator, (Duyesen and Pearson 1976, 1980; Grillner and Rossignol 1978b; Hiebert et al. 1996); and be used continuously or intermittently to update the motor output or internal state [e.g., regulation around a desired state in the manner of servo assist (see Stein 1974) or using some additional type of internal model in control].

In our experiments, several of the mechanisms outlined in the preceding text could contribute to the effects seen after deafferentation. Minimally we believe homonymous feedback and regulation of muscle properties (e.g., Nichols and Houk 1976) must be invoked to account for our data. However, it is to us unlikely that some of the altered muscle balances seen here after deafferentation do not also involve heteronymous effects, both excitatory and inhibitory. Heteronymous feedback effects have been shown to be quite widespread in the limb and...
to regulate global mechanical properties of the limb (e.g., Bonasera and Nichols 1996; Misaszek and Pearson 1997; Misaszek et al. 1995). The mechanical benefits of double-joint muscles and multijoint feedback control have been argued strongly (Gielen 1993; Hogan 1985; Lacquaniti et al. 1992; McIntyre et al. 1996).

Proprioceptive feedback may play additional roles in the spinal control of wiping trajectories. For example Koshland and Hasan (1994) and Karst and Hasan (1991a,b) have described initial muscle selection rules for planning of human planar arm movements based on initial joint configuration and target location. In addition, some roles for feedback in the frog may resemble roles of proprioceptive feedback in human trajectory formation, namely the regulation of joint coordination and the on-line control interaction torques (Ghez and Sainburg 1995; Gordon et al. 1995; Sainburg et al. 1995). The collapse of joint staggering during wiping trajectories seen after deafferentation is reminiscent of the observations of Sainburg et al. (1993) in humans with loss of proprioception. The increased path length and curvature of the end point (i.e., ankle) after deafferentation is also similar to humans without proprioception. Finally, some of the overshoot effects on approach of the target limb may be related to the loss of precise deceleration of the limb. Deceleration may be difficult to control in an exclusively feedforward manner (Lin and Rymer 1993), although this may be possible with practice (Bizzi et al. 1976; Sainburg et al. 1995).

Despite the arguments in the preceding text, distinguishing specific controls and nonspecific effects is problematic in total deafferentation or in complete loss of specific modalities. On the one hand, it is known that spinal pattern generators may antidromically activate afferents via primary afferent depolarization (Gossard et al. 1991). This could have the effect of reducing the apparent role of afferents compared with their actual significance in the intact condition. Alternatively, radical reorganization of the program and changes could occur because feedback is missing, but in the intact condition, feedback could be used largely for monitoring execution rather than controlling it. Because of the complexity of these possibilities, we take the present study to indicate that one or more of the more complex mechanisms of proprioceptive afferent use has a functional role in trajectory control during wiping but not to firmly establish any specific role. Future work will explore this.

**Motor-pattern composition**

The motor pattern during hindlimb wiping consisted of three waves of EMG activity. The first wave of activity included primarily biceps (iliofibularis), semitendinosus, and sartorius, muscles that all generate flexor torque at the knee. The second wave of activity included primarily rectus internus, semimembranosus, and adductor magnus, large muscles that all generate extensor torque at the hip. A final wave of knee extensor activity closely followed target limb contact. The latency between the first two waves of EMG activity was one of the parameters used to categorize wiping “styles.” Joint coordination was directly related to this measure of motor-pattern latency. For instance, frogs with longer latencies had increased joint staggering between the knee and hip.

A substantial fraction of the variation in kinematic change seen among frogs after deafferentation was described by the measure of either joint staggering or motor-pattern latency when feedback was intact. Frogs with longer latencies and/or increased joint staggering showed larger reductions in the latency between the first two muscle groups and in the degree of joint staggering. Those frogs with synchronous motor patterns (i.e., EMG coactivation strategies) and knee-hip motion showed little to no effect of deafferentation and thus appeared to operate mainly in a feedforward manner.

In addition to changes in motor-pattern latency, some of the variation in kinematic change seen after deafferentation could be related to changes in the peak amplitude of muscle activities. Spinal frogs were shown to fall into three groups based on the degree of change in ankle-path straightness after deafferentation: no change, moderate change and severe change. As mentioned previously, those frogs with no change operated mainly in a feedforward manner. The other two groups were associated with changes in the peak amplitude of activity of muscles in either the first group or the second group. Frogs with moderate changes in path straightness exhibited decreased amplitudes of activity of BI and SA (i.e., muscles of the first muscle group). Frogs with more severe changes in path straightness exhibited in addition an increased amplitude of RI/SM/AD activity (i.e., muscles of the 2nd EMG group). These frogs also showed the large increases in hip velocity and knee-joint reversals. The increased hip velocity may be related to generating increased interaction torques at the knee and to the knee-joint reversals.

The independence of the different motor-pattern changes after deafferentation was largely unexpected. Magnitude and latency changes of the initial two muscle groups could be considered independently. Taken together these observations are consistent with feedback regulation of the amplitude and timing of component muscle groups that comprise wiping. The combination of an active group of muscles (either entire muscles or muscle compartments) plus the activated population of afferents and reflex pathways acting as a unit has been termed a “task group” (Loeb 1985), or, in the case of invariant multijoint force patterns, a primitive (Bizzi et al. 1991; Giszter et al. 1991, 1993; Mussa-Ivaldi et al. 1994). Thus some of the motor-pattern changes seen here may reflect the absence of the feedback component of the movement primitives that comprise wiping.

**Individual variations**

The variability observed in the susceptibility to deafferentation in spinal frogs is interesting and deserves discussion. Loeb (1993) showed that the strength and form of various reflexes during locomotion in both intact and spinal cats exhibited interanimal variability. Repeated experience can lead to adjustments in reflex gain that may become embedded within the spinal cord (Chen and Wolpaw 1995, 1997; Chen et al. 1996; Whelan and Pearson 1997; Whelan et al. 1995). Thus frogs may differ in experience. It is worth noting that several amphibious animals are known to be able to vary their reflex states and gains based on environment (e.g., ghost crabs) (Hoyle 1976). Finally, transition is known to affect reflex strengths in mammals, and there may be differential effects mediated by factors outside the CNS. For example, Cope et al. (1980) showed that the strength of a reflex pathway in a portion of the spinal cord, isolated from rostral CNS by complete spinal
transection, could be modified by additional lesions of the rostral CNS despite the lack of direct communication between these portions. Presumably autonomic or other such factors could account for this. In our experiments, we believe such outside effects are likely to be uniform among frogs because only a single transection, which was always at the same location, was used in all frogs.

The finding that susceptibility to deafferentation varied based on motor-pattern variations with feedback intact suggests that reflex gains may be adjusted based on “motor style.” For instance, frogs with synchronous motor-patterns (i.e., knee flexor group and hip extensor group activated together) used a coactivation strategy to move the end point to the target. These frogs showed little change in the phasing or magnitude of the component muscle activities. Frogs that exhibited more phase-staggered motor patterns (e.g., distinct knee flexor EMG burst followed by a hip extensor burst) showed larger deficits after deafferentation. These deficits could be explained by magnitude and phasing changes of the knee flexor and hip extensor EMG bursts (see preceding text). It is not clear if and how the range of motor-pattern types (i.e., from coactivation to staggered strategies) are related to optimizing different mechanical, metabolic, or accuracy parameters of the wipe when feedback is intact (see Loeb 1993 for discussion).

Conclusion

Our data show a role of proprioceptive feedback in regulating both motor pattern and the resultant trajectory of the wiping limb. In particular, the specific trajectory of the end point or the effector (i.e., the initial direction, the path structure, and the site of target contact) depends on proprioceptive feedback. The dependency on proprioceptive feedback appears graded depending on the trajectory form and the pattern of joint coordination when feedback is intact. Trajectory variations among frogs with intact feedback are related to variations in the phasing of component muscle groups that comprise the motor pattern. In addition to the maintenance of phasing between muscle groups, the amplitude of activation of muscle groups is related to the control of movement. Frogs with intact feedback are related to variations in the amplitude of activation of muscle groups (excitatory or inhibitory control).

Special thanks to M. R. Davies for support, assistance, and helpful comments. We thank reviewers for helpful comments and suggestions.

This work was supported by ASRI grants and National Institutes of Health Grant NS-34640 to S. F. Giszter and by ASRI fellowships to W. Kargo, who also was supported by NIH Rehabilitation Training Grant 5T32 HD-07467-05 to M. Murray.

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Received 10 December 1998; accepted in final form 1 November 1999.

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