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Hindlimb Endpoint Forces Predict Movement Direction Evoked by Intraspinal Microstimulation in Cats

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Abstract

We measured the forces produced at the cat's hindpaw by microstimulation of the lumbar spinal cord and the movements resulting from those forces. We also measured the forces and movements produced by co- and sequential activation of two intraspinal sites. Isometric force responses were measured at nine limb configurations with the paw attached to a force transducer. The active forces elicited at different limb configurations were summarized as patterns representing the sagittal plane component of the forces produced at the paw throughout the workspace. The force patterns divided into the same distinct types found with the femur fixed. The responses during simultaneous activation of two spinal sites always resembled the response for activation of one of the two sites, i.e., winner-take-all, and we did not observe vectorial summation of the forces produced by activation of each site individually as reported in chronic spinal animals. The movements produced by activation of each of the sites were consistent with the force orientations, and different movements could be created by varying the sequence of activation of individual sites. Our results highlight the absence of a vectorial summation phenomenon during intraspinal microstimulation in decerebrate animals, and the preservation during movement of the orientation of isometric forces.

Index Terms

Dynamics; force measurement; functional electrical stimulation; legged locomotion

I. Introduction

Activation of neuronal circuits in the spinal cord is a potential means to simplify the control challenges of synthesizing standing and walking by coordinated stimulation of multiple single muscles. A number of complex movements, including locomotion, are organized at the level of the spinal cord and can be generated independent of any descending inputs [1]–[3]. Such spinal circuits may be available for artificial electrical stimulation as a means to restore the functions that they control.

In the cat, the responses to intraspinal microstimulation of the lumbar spinal cord have been studied at the level of limb kinematic responses, muscle activation, or single joint torques with stimulation delivered in the ventral portion (ventral lamina VII, and laminae VIII–IX)

of the gray matter [4]–[11]. Alternating sequential activation of sites producing flexor or extensor responses produces locomotor-like movements [4], [8], [9], [12], [13], and stimulation in the dorsal columns or dorsal grey of the L3/L4 segments produced treadmill locomotion in chronic spinal cats, especially when delivered in combination with pharmacological agents [14]. Similar bouts of locomotion were evoked by stimulation in the ventral aspect of more caudal portions of the spinal cord [15].

Our own studies have concentrated on measurements of the isometric force patterns produced at the limb endpoint by intraspinal microstimulation in the cat lumbar spinal cord [16]. As in other species [17], [18], we found that the force patterns produced at the endpoint of the limb were of a limited number of types, suggesting a modular organization of the spinal motor output [19]. Further, evidence from reflex movements in the frog [20] and postural adjustments in the cat [21] and human [22] suggests that the motor system does indeed create movement by superposition of individual modular force patterns [23]. This apparent modularity and the observation that the endpoint forces evoked by co-activation of two spinal sites sum vectorially [18], [24], [25] suggest that movement and stable posture could be created by grading the co-activation of a limited number of spinal sites, each site producing a different force pattern.

In the present study we extended on our previous measurements of the isometric forces produced at the limb endpoint by intraspinal microstimulation by 1) determining the isometric force patterns obtained at the paw with the femur free to move, 2) measuring the isometric forces produced by co-activation of two spinal sites, 3) measuring the forces and movements produced by stimulation of single or multiple intraspinal sites, and 4) comparing the movements obtained with intraspinal stimulation with the predictions of a biomechanical model of the cat hindlimb subjected to a scaled version of the measured isometric forces. The isometric force patterns obtained at the endpoint of the limb with the femur free to move (i.e., a three-link system) were comparable to the force patterns we measured previously in the two-link system of the shank and paw with the femur fixed [16]. The endpoint force patterns produced by co-activation of individual spinal sites did not sum vectorially, but rather exhibited a winner-take-all response. Further, the movements of the endpoint in the sagittal plane correlated with the prediction of the limb model driven by the measured isometric forces, indicating that the orientations of force vectors measured isometrically were maintained during movement. This result, combined with the absence of vectorial summation during co-activation of spinal sites, suggests that sequential activation of spinal sites may be preferable to co-activation of sites to create complex movement patterns.

II. Materials and Methods

A. Experimental Preparation

Results from seven adult male cats (domestic short hair, 2.8–4.0 kg) are reported in this study. All animal care and experimental procedures were according to NIH guidelines and were reviewed and approved by the Institutional Animal Care and Use Committee of Case Western Reserve University.

Animals were initially anesthetized using ketamine HCl (Ketaset, 15–30 mg/kg, IM) given in combination with atropine sulfate (0.05 mg/kg, IM). The animals were then intubated and maintained at a surgical level of anesthesia with halothane (0.5%–2% in O₂) until completion of decerebration, at which time anesthesia was discontinued. The cephalic vein was catheterized to administer fluid and drugs during the procedure. Animals were ventilated to maintain expired CO₂ at 3%–4%, body temperature was maintained between 37°C and 39°C using thermal pads, warm 0.9% saline with 8.4 mg/ml sodium bicarbonate

and 5% dextrose added was administered IV (10–15 ml/kg/hr), and carotid blood pressure was monitored throughout the experiment.

A dorsal laminectomy was made from L4–L7 to expose the lumbosacral spinal cord and spinal roots. Dexamethasone (2 mg/kg, I.V.) was administered at the completion of the laminectomy and every 6 h thereafter to reduce edema in the spinal cord. The contralateral (left) limb was denervated by transecting the sciatic, femoral and obturator nerves. This denervation was performed to prevent mechanical coupling of motor responses from the contralateral limb (through the pelvis) to the force sensor to which the ipsilateral limb was attached. Following denervation of the contralateral limb, the animal was transferred to a custom stereotaxic frame. The skull and spinal vertebrae (L3 and S1) were clamped rigidly to the frame. The animal's pelvis was held with bone pins, and the paw of the right hindlimb (ipsilateral to intraspinal stimulation) was attached to a small bar mounted on a six-axis force transducer (nano17, ATI Industrial Automation, Apex, NC) by a rotational joint. The force transducer was mounted at the end-point of a planar robot. The robot could hold the paw isometrically during force measurements, or be free-moving during motion measurements. The hindlimb formed a three-link assembly, which allowed hip motion in addition to knee and ankle motion. Once the animal was securely mounted in the frame, a postmammillary decerebration [26] was performed under halothane anesthesia. The brain rostral to the transection was removed (including cortex and thalamus) and the skull packed with Surgicel, Avitene, and agar to control bleeding. Dextran was administered if needed to maintain blood pressure, and anesthesia was discontinued once the decerebration was completed. The dura was opened to expose the spinal cord, which was bathed in warm mineral oil.

B. Data Collection

Isometric Force Patterns Resulting From Single Site Intraspinal Stimulation—

Isometric motor responses were elicited by intraspinal microstimulation with trains of biphasic current pulses (train duration: 0.5 s; frequency: 40 Hz; pulse duration: 100 μ s; pulse amplitude: 50–100 μ A) delivered via iridium wire microelectrodes (IS-300, diameter 50 μ m, Huntington Medical Research Institutes, Pasadena, CA). Endpoint forces were evoked by stimulating along dorsal to ventral penetrations (in increments of 200 μ m), at a series of positions spanning L5–L7 rostrocaudally and from the medial to lateral grey matter. At selected depths along each penetration the limb was moved to nine different locations on a 6 cm $\times$ 6 cm grid centered on a mid-stance position (Fig. 1), and evoked forces were recorded at each endpoint location while stimulation parameters and electrode position were kept constant. The isometric forces and motion produced at the paw were sampled at 2000 Hz. To ensure that forces were stable over time, we repeated the force measurement at the midstance position after forces at the other eight grid positions were collected. Differences in magnitude and orientation were compared between the initial and final measurements at midstance position.

Isometric Force Patterns Resulting From Co-Activation of Two Spinal Sites—

In six animals we conducted co-stimulation experiments via two electrodes inserted into the spinal cord simultaneously but independently. We measured the responses produced by individual stimulation of each spinal site, and the forces produced by simultaneous stimulation of both sites with interleaved pulse trains. The stimulation parameters, stimulation sites, and endpoint recording locations were as for the single site isometric recordings described above.

Movements Resulting From Single Site Intraspinal Stimulation—In five animals we also measured the motion of the endpoint produced by intraspinal microstimulation of a

single spinal site. Movements were executed against the robot in all cases; for two of the spinal sites, the robot was programmed to counterbalance its own weight, while for the other five sites, the robot was programmed to behave as a linear spring with varying equilibrium position and stiffness. The equilibrium position was chosen to hold the limb in a midstance position at rest, and stiffness ranged from 25–200 N/m. We analyzed both the distance of movement (from initial position to furthest point reached during stimulation) and the direction of the movement in relationship to the orientation of the isometric forces.

Movements Resulting From Sequential Activation of Two Spinal Sites—In three animals we measured the movements produced by sequential activation of two intraspinal sites; one produced a flexion response and the other an extension response against the robot programmed to behave as a linear spring. The spring equilibrium position was positioned dorsal to the foot, and generated a force ($\sim 1 - 2$ N) that held the limb in a midstance position at rest. This slightly flexed starting position was chosen to permit the observation of the extension movements produced by activation of extensor responses.

Isometric Force Patterns Resulting From Activation of Individual Muscles—At the completion of the spinal mapping experiments we also measured the forces produced by stimulation of single muscles in three animals. The muscles were activated with trains of biphasic current pulses (train duration: 0.5 s, frequency: 40 Hz, pulse duration: 100 μ s, pulse amplitude: 1–5 mA) delivered through fine bifilar electrodes implanted in each muscle. Force measurements were obtained for 11 muscles: three *tibialis anterior* (TA), two *biceps femoris posterior* (BFP), three *vastus lateralis* (VL), and three *medial gastrocnemius* (MG). Muscles that did not produce forces above ≈ 0.2 N with pulse amplitudes of 4 mA were not studied. Forces were measured as for the intraspinal stimulation isometric force measurements.

C. Data Analysis

Isometric Force Pattern Reconstruction—The forces measured at the nine positions of the foot were used to calculate the forces acting at the endpoint throughout the workspace encompassed by those points. The endpoint forces were represented as 2-D vectors in the sagittal plane, and patterns representing the force vector orientations and magnitudes throughout the workspace were constructed (Fig. 1, also see [16]). The workspace was divided into triangles, and the forces within a triangle were calculated by linear interpolation based on the force vectors measured at the vertices of the triangle. The forces at each corner of each triangle yielded one force vector (F_x, F_y), as well as one position (x, y) coordinate. Combining the three corners of a triangle yielded a system of six unknowns and six equations relating the forces at any position within a triangle to the forces at the vertices. The triangulation was constructed to minimize the distance between the interpolated points and the triangle vertices. Only the active force components (total forces minus the passive forces recorded prior to the onset of stimulation) were analyzed.

Isometric Force Pattern Classification—We divided the active force patterns obtained with intraspinal microstimulation into groups using cluster analysis methods. Cluster analysis partitions a set of objects into a number of disjoint groups so as to optimize a mathematical criterion. In this case, we used the squared Euclidean distance between cases as our partitioning criteria. A case was defined as the set of forces (F_x, F_y) at each of the nine positions for one force pattern, i.e.,

$$\begin{aligned}
&\text{Case 1: } \{F_{x1}^1, F_{y1}^1, F_{x2}^1, F_{y2}^1, F_{x3}^1, F_{y3}^1, \dots, F_{x9}^1, F_{y9}^1\} \\
&\text{Case 2: } \{F_{x1}^2, F_{y1}^2, F_{x2}^2, F_{y2}^2, F_{x3}^2, F_{y3}^2, \dots, F_{x9}^2, F_{y9}^2\} \\
&\quad \vdots \\
&\text{Case n: } \{F_{x1}^n, F_{y1}^n, F_{x2}^n, F_{y2}^n, F_{x3}^n, F_{y3}^n, \dots, F_{x9}^n, F_{y9}^n\}
\end{aligned}$$

Thus, the squared Euclidean distance between cases was defined as

$d_{ij} = \sum_{k=1}^9 (F_{xk}^i - F_{xk}^j)^2 + (F_{yk}^i - F_{yk}^j)^2$, i.e., the squared sum of the differences in the x and y forces measured at each position between case i and case j . To prevent larger forces from dominating the distance measure, we normalized the forces so that the largest measured force vector within each force pattern had a magnitude of 1. We determined the number of types of force patterns using hierarchical cluster analysis (Ward's method), and grouped the cases based on the results of the agglomeration schedule.

Analysis of Isometric Force Responses to Co-Activation of Two Spinal Sites—

The active force patterns evoked by stimulation of two individual intraspinal sites, $\mathbf{F}_A$ and $\mathbf{F}_B$, and those evoked by co-stimulation of the same two sites, $\mathbf{F}_{AB}$, were constructed as described above. The relationship between the individual and co-stimulation responses was tested against three hypotheses.

1. Linear summation hypothesis: the response during co-stimulation was the scaled vector sum of the individual force responses, i.e., $\mathbf{F}_{AB} = s[\mathbf{F}_A + \mathbf{F}_B]$, where s was obtained via least-squares regression. This relationship was demonstrated in the spinal frog [24], [25] and rat [18].
2. Winner-take-all hypothesis: the response during co-stimulation was a scaled version of one of the individual responses, i.e., $\mathbf{F}_{AB} = \min \|\mathbf{F}_{AB} - s(\mathbf{F}_A \text{ or } \mathbf{F}_B)\|$, with s for each individual response obtained via least-squares regression. This hypothesis occurred at 58.5% of the sites studied in spinal frogs [24].
3. Weighted summation hypothesis: the response during co-stimulation was a weighted vector sum of the individual force responses, i.e., $\mathbf{F}_{AB} = s_1\mathbf{F}_A + s_2\mathbf{F}_B$, where s_1 and s_2 are the scaling factors for each of the individual responses, again obtained by least-squares regression. Note that linear summation is a special case of this more general hypothesis, with $s_1 = s_2$ and winner-take-all is another variant of this more general hypothesis with either $s_1 \gg s_2$ or $s_2 \gg s_1$.

The average force vector residuals (from the nine hindlimb positions) were compared between each of the three models of force pattern combination using t -tests. The quality of the model fits to the actual co-stimulation response was assessed using the average ratio between the measured forces and model predicted forces at each of the measured hindlimb positions and angular difference in force orientations at each of the measured hindlimb positions [25]. The average force magnitude ratios were compared using the t -test, and the V test [27] was used to compare the force vector orientation.

Analysis of the Movements Produced by Intraspinal Stimulation: Single Site Activation and Sequential Activation of Two Spinal Sites—

For movements produced by activation of a single site, we measured the size of the evoked movements (from initial position to furthest point reached during stimulation) and the direction of the movements in relation to the orientation of the isometric forces evoked by stimulation of that site.

For movements created via sequential activation of two sites (one producing a flexor response and the other producing an extensor response), we calculated the movement time and the maximum velocity of these movements. We then compared the movements and their associated parameters (range, velocity, duration) to the average step cycle of a normal cat walking at a comfortable speed of 0.4 m/s on a motorized treadmill. The right hindlimb and forelimb kinematics were captured at 300 frames/s using a Vicon Motion Analysis system (Vicon Peak, Lake Forrest, CA) (see [28] for full methods).

Biomechanical Modeling of the Movement Produced by the Measured Isometric Force Patterns—

We compared the movements produced by activation of a single stimulation site to the forward dynamic integration of a planar three-link model of the cat hindlimb submitted to a scaled version of the measured isometric forces. The model was implemented in MATLAB (The Mathworks Inc., Natick MA) to represent a single hindlimb with three rigid segments (thigh, shank, and foot), which were attached with revolute joints at the knee and ankle, with the femur fixed to ground at the pelvis with another revolute joint. The mass and length of each segment were determined from published studies [29]. The system followed Lagrange's equation of motion for a three-link manipulator

$$\tau = M(\theta)\ddot{\theta} + h(\theta, \dot{\theta}) + g(\theta)$$

where θ is the matrix of joint angles, M is the inertial force term, h is the centrifugal and Coriolis force term, g is the gravitational force term, and τ is the total joint torque matrix. Total joint torque was calculated by $\tau = \tau_i - \tau_d + \tau_a$, where τ_i was the end-point force vector converted to a joint torque matrix, τ_d was a damping torque, and τ_a was a range of motion constraint function that modeled the passive torque at the joint at the limits of the physiological range of motion. The damping torque was given by

$$\tau_d = \tau_i(1 - e^{-k|\dot{\theta}|})$$

where τ_i was the end-point torque (calculated from the isometric endpoint force pattern) and k was a constant determined by optimization. The range of motion constraint function

$$\tau_a = c \dot{\theta} \left(\frac{\text{flex} + \text{ext} - 2\theta}{a|\text{flex} - \text{ext}|} \right)^b$$

was setup so that the added constraining torque was not a significant part of the total torque in the middle of the range of motion (parameters $a = 0.6$, $b = 5$, and $c = 3.0e^5$). The parameters *flex* and *ext* were the flexion and extension limits of the joint in radians.

The temporal change in endpoint force magnitude (and hence torque) with stimulation was modeled using the function

$$F(t) = f_s F_{0.5s} t$$

where f_s was a scaling parameter determined by optimization and $F_{0.5s}$ was the static force measured 0.5 s after onset of stimulation. We used MATLAB's built-in 3-D linear interpolation function to estimate the endpoint force at any point within the grid.

For each trial, the endpoint of the model limb began at the initial experimental position of the cat toe. Since the initial angles of the joints were not measured during the experimental trials, these parameters were varied during optimization. The equations of motion were integrated through a variable order ordinary differential equation solver using numerical differential formulas. At each time step the output of the solver gave the joint angles for the next time step.

At each time step in the integration, the model's endpoint position was compared to the experimental position data and an error was calculated as the sum of the squared difference in x -position and the squared difference in y -position. The three initial joint angles, endpoint force scaling constant, and the constant k from the damping function were the free parameters that minimized the cumulative error for the entire time of integration. This allowed us to identify the most likely initial limb configuration, force profile, and damping term.

III. Results

The forces evoked at the endpoint of the hindlimb by intraspinal microstimulation were measured in seven decerebrate cats. Force patterns were obtained for 27 intraspinal sites over 18 penetrations, 19 sites ipsilateral and eight sites contralateral to the measured limb. Depth of sites from which force patterns were measured was from 400 to 3000 μm from the dorsal surface. Force patterns were evoked from sites that produced stable force vectors with repeated stimulation and over a range of depths of approximately 600 μm .

The time course of the force vectors evoked by microstimulation of the lumbar spinal cord was similar to our published report with the femur fixed [16], and the orientation of the force vectors evoked by stimulation was consistent during the stimulation train. The latency between stimulation onset and force onset was typically 50–100 ms, and forces often persisted for several seconds beyond the end of the stimulation period. The force vectors of the initial and final responses at the midstance position differed by $4.3 \pm 7.8^\circ$ and 0.37 ± 0.35 N for the individual sites, and by $7.7 \pm 3.8^\circ$ and 0.25 ± 0.22 N for the co-stimulation experiment sites. Initial average force at the mid-stance position was 1.3 ± 0.93 N for the individual sites and 1.6 ± 1.1 N for the co-stimulation experiment sites. Based on the very small differences and standard deviations of angular direction we conclude that forces were more stable in direction than in magnitude.

A. Types of Force Patterns Evoked by Single Site Activation

The 27 patterns of endpoint forces evoked by intraspinal microstimulation were of three types: caudal flexion (CF) responses that pulled the limb backwards and upwards towards the body, caudal extension (CE) responses that extended the limb backward, and rostral extension (RE) responses that extended the limb forward (Fig. 2, see also [16]).

All three responses were also observed with the femur fixed [16] where a rare fourth response (rostral flexion) was also obtained. The patterns were divided using hierarchical cluster analysis based on the squared differences between forces measured at the same position, summed across the workspace. Caudal flexion was the most common response (16 of 27 patterns), followed by rostral extension (8 of 27) and caudal extension (3 of 27) (Table I).

This distribution was significantly different (Chi-square test) than the distribution of force response types obtained with the femur fixed (Table II) [16]. The main differences were in the proportions of rostral and caudal extension responses obtained in the two conditions: more rostral extension responses were obtained with the femur free than with the femur fixed. This was accompanied by a reduction in the proportion of caudal extension responses, while the proportion of caudal or rostral flexion responses remained relatively unchanged. The spinal sites were located in the dorsal horns of the lateral grey matter. Flexion responses were mostly observed for stimulation in the more dorsal laminae while extensor responses resulted from ipsilateral stimulation of sites in more ventral laminae or contralateral sites in dorsal laminae. Overall, this topography was consistent with our previous observations [16], [30].

Forces evoked by activation of individual muscle were also measured in three decerebrate cats. The 11 (3 TA, 3 MG, 2 BFP, 3 VL) muscle force patterns grouped into patterns similar to the responses evoked by intraspinal stimulation (Fig. 2). The MG muscles produced CE responses, the VL produced RE responses, BFP produced CF responses, and TA produced a response resembling the CF responses, although the forces were more vertical than caudally oriented (compare the left and right top panels of Fig. 2) (see also [16] and [31] for further experimental evidence and biomechanical modeling of the force patterns produced by activation of individual muscles).

B. Force Patterns Evoked by Co-Activation of Two Intraspinal Sites

We conducted six co-stimulation experiments where we measured isometric endpoint force responses evoked by two individual intraspinal sites and the isometric endpoint force responses evoked by co-stimulation of both sites. One ipsilateral site and one contralateral site were used in four of the six cases, while two ipsilateral sites were used in the remaining two cases. Stimulation depths ranged from 600 to 1000 μm for the ipsilateral and contralateral sites, and electrode penetrations were > 1 cm apart from one another in all cases. All sites were within the L6/L7 spinal cord and 600–1500 μm from the midline. We made every effort to obtain individual site responses that were of different types so that we could distinguish between the linear summation and winner-take-all hypotheses, and we succeeded in four of the six cases. In contrast, comparison of two similar individual responses to the co-stimulation response can cause ambiguity between the linear summation and winner-take-all hypotheses [24].

An example of the responses evoked by stimulation of two intraspinal sites is presented in Fig. 3. The ipsilateral electrode produced a caudal flexion response (F_A), while the contralateral electrode produced a caudal extension response (F_B). The forces obtained during co-stimulation of both sites, as well as the optimal fits for each of the three models: linear summation, winner-take-all, and weighted sum, are also illustrated. The parameters for the best fit of each of the models were $s = -0.045$ for the linear sum, $s = 1.56$ for the winner-take-all with the ipsilateral site winning, and $s_1 = 1.60$ (ipsilateral site) and $s_2 = 0.03$ (contralateral site) for the weighted summation. The negative scaling coefficient for the linear summation is indicative of how poor the fit was for that model, and the average residual for the forces (x and y force coefficients) was 0.586 N (corresponding to about 95% of the co-activation response). Both the winner-take-all and weighted sum models reproduced well the actual co-stimulation response, and the average force residual was ~ 0.1 N for both models. In the weighted sum model, the scaling coefficient for the contralateral response (F_B) was very low, indicating that the response evoked from the contralateral site did not contribute to the response during co-activation of the two sites. Thus, this is an example of a winner-take-all combination of force responses.

This example was representative of results from six response sets collected across five experiments. For all six cases, the lowest or not significantly higher average force vector residual was obtained for the winner-take-all model. In four of the six cases, the residual of the weighted summation model was not significantly different than the residual of the winner-take-all model, but the scaling factor for the second site was low or even negative. In one case, the linear, winner-take-all, and weighted summation models all had similar residuals. The scaling factor s of the winner-take-all model ranged from 0.43 to 2.71 (1.26 ± 0.81 , not significantly different than 1.0). For all six cases, the winner-take-all model output (scaled single site response) showed no significant difference in force magnitude ratio (t -test, $\alpha = 0.05$) or force vector orientation (V test, $\alpha = 0.05$) from the actual co-stimulation response.

In the four cases involving combination of ipsilateral and contralateral stimulation sites, the response from the ipsilateral site was the winner in the winner-take-all model. The residuals for the contralateral response fit to the co-activation response were significantly higher than the residuals for the ipsilateral fit for all four cases (t -test between means). For the two cases involving combination of two ipsilateral sites, the residuals were about twice as large for the “losing” ipsilateral response (significantly higher than the ipsilateral fit residuals for both cases, t -test) and the force vector orientation was significantly different (V test, $\alpha = 0.05$) from the actual co-stimulation response. In summary the residuals for the “losing” response fit were significantly higher than the residuals for the “winning” response fit in all cases.

C. Movements Produced by Intraspinal Stimulation: Single Site and Sequential Activation of Two Spinal Sites

We measured the movement of the endpoint produced by stimulation of a single spinal site for seven sites (five were ipsilateral to the side of movement, two were contralateral). Movements were executed against the robot in all cases. While stimulus train durations were often increased in these trials to increase force magnitude, observations during isometric trials showed that force directionality was not affected by stimulus train duration. We analyzed both the size of the evoked movements (from initial position to furthest point reached during stimulation) and the direction of the movements in relation to the orientation of the forces. Movements spanned from 0.7 to 19.1 cm with an average distance of 6.0 ± 5.1 cm ($n = 36$ motions). Several factors influenced the size of the movements, including the duration of the stimulus train and the stiffness of the spring against which the paw was moving. Movements tended to be larger with more prolonged activation and more compliant springs.

For two of the individual sites where we measured movements from different starting positions or for different stimulation levels but under the same endpoint load, we compared the direction of each movement (measured as the angle between initial and final positions) with the direction of the vector joining the initial position of that movement with the position obtained at the end of stimulation for the largest movement evoked by stimulation at that site. The differences between the two vectors for the eight movements over two sites ranged from -38° to 29° (mean $\pm$ sd: $0.51^\circ \pm 20^\circ$, not statistically different than 0° , V test with $\alpha = 0.05$). Even if no point of convergence or zero net forces was measured in the sampled workspace, the movements produced by activation of the spinal sites were directed towards a single point that was not affected by stimulus amplitude or duration of activation.

In three experiments we measured the movements produced by sequential activation of sites that produced a flexion response (CF) and an extension response (RE in two and CE in one). Fig. 4 illustrates the movements evoked by sequential activation of one flexor and one extensor response. Two different movements were created by reversing the order in which the sites were activated. One movement was created by initially activating the flexion

response, and then the extension response, while the second movement was created by activating the extension response followed by the flexion response. While activation of the CF response first produced a caudal and up movement of the leg, the direction produced by the CF site was more vertically directed when activated from the more rostral and down initial position following activation first of the RE response. This was consistent with the fact that the flexor forces were oriented parallel to one another. The most extended positions obtained with activation of the RE sites were very similar, although the leg extended further with the limb starting from a less flexed initial position, i.e., when the extension response was activated first.

The movements time and the maximum velocity of these movements were longer and slower, respectively, than those measured during treadmill walking (see Fig. 5). While a step on the treadmill was completed in about 1 s, the flexion–extension movement created extended over 8 s for a shorter range of motions. The maximum velocity obtained was about a 1/4 of the velocity obtained during walking. While we made no attempt to maximize movement speed by increasing stimulation amplitude, the combined results of Figs. 4 and 5 indicate that movements evoked by intraspinal microstimulation may be limited in speed and range of motion when compared to natural movements.

D. Comparing Movements Simulated With a Forward Dynamic Model to Movements Evoked by Single Site Intraspinal Microstimulation

The movement obtained via integration of the forward dynamic model, subjected to the measured active forces, was compared to the actual movement of the hindlimb endpoint acting against the robot programmed as a linear spring. The endpoint stayed within the measured workspace for 11 trajectories, with spring stiffness ranging from 40 to 200 N/m. Fig. 6 shows the total forces measured and the movement produced moving against a 100 N/m spring centered on the measured workspace (marked with an X). The average error between measured and model movements was 0.46 ± 0.24 cm. For the 11 trajectories simulated, the average position error was 0.87 ± 0.66 cm. While the optimization matched the movements relatively well, the velocity profiles differed markedly as shown in the bottom panel of Fig. 6. The result was not unexpected since the optimization criteria did not take velocity into account, but focused solely on matching position.

IV. Discussion

The goal of this study was to characterize the endpoint forces and movements elicited by intraspinal microstimulation of the cat lumbar spinal cord. We found that the hindlimb endpoint forces grouped into a small number of directionally arranged patterns, as observed previously with the two-link system of the lower shank and paw [16], suggesting a modular organization to the spinal cord motor output. In contrast to studies in frogs and rats [18], [24], [25], we did not observe that co-stimulation of individual sites produced vectorial summation of the forces produced at each of the individual sites, but rather responses evoked by co-stimulation exhibited a winner-take-all behavior. Subsequently, we measured movements produced by sequential activation of the spinal sites, and found 1) the isometric force patterns to be predictors of the movements produced by activation of the sites, and 2) that different movements could be constructed by varying the order in which sites were activated.

A. Absence of Vectorial Summation During Co-Activation of Two Spinal Sites

Vectorial summation did not occur at any of the six combination of sites tested. In rats, vectorial summation was observed, but the percentage of sites exhibiting winner-take-all responses was not reported [18]. In the frog, 87.8% of the combinations (41 tested) could be

explained by linear summation, and winner-take-all fitted the experimental data in 58.5% of the sites [24]. As the sum of the percentages indicates, a number of the co-activation responses could fit both hypotheses because the individual responses were similar. However linear summation provided a better fit in 80.5% of the cases, which never occurred with our co-activation responses. The probability of obtaining six combinations producing a better fit for winner-take-all with the same underlying binomial distribution is less than 0.01%. Our results clearly suggest that the responses during co-activation are different in nonspinal animals, or in larger mammals. Since four of our co-activation experiments involved one ipsilateral and one contralateral site, an inhibitory mechanism from the ipsilateral to contralateral side (as in the crossed-extensor reflex) may be responsible for the difference, yet the results were similar for the two cases where both spinal sites were ipsilateral. The presence of linear summation of force responses during co-activation of two spinal sites in both spinalized frogs and spinalized rats also suggests that supraspinal influences at the level of the brain stem/cerebellum (since cortex and thalamus were removed) may modify the interactions between responses evoked by stimulation at different spinal sites or that chronic spinalization modifies these interactions. Evidence in the frog suggests that modularity of motor output in response to stimulation of the higher centers or cutaneous reflex activation is preserved in animals with intact/partial brainstem [32], [33], although the combination rules of multisite intraspinal microstimulation were not studied in those animals.

B. Forces and Movements

As Newtonian mechanics predicts, movements were in the direction of the forces generated at the endpoint (measured isometrically in this study). These results would suggest that, as in the frog where actual endpoint motion follows the movement of the isometrically measured point of zero forces (termed the “equilibrium point trajectory”) [17], the directionality of the forces is preserved during unobstructed movement. However, the amplitude of movement may be influenced by damping and other factors (reflexes, muscle length, etc.) not present under isometric conditions. A simple forward dynamic simulation of the cat hindlimb, actuated with the measured active forces, moved along a path that lay within 1 cm of the actual trajectories evoked by intraspinal microstimulation. This result supports the hypothesis that the direction of isometric forces is maintained during actual movements, i.e., a caudal flexion response remains a caudal flexion response. The direction of the endpoint force and initial acceleration were not always aligned due to interaction torques in the linkage formed by the upper leg, lower leg, and foot [34]. Further, the lack of congruence between the velocity profiles from the model and experiments suggests that the time course of the force magnitude may vary from that measured isometrically, a result observed in frogs where force direction was preserved despite changes in amplitude (from isometric values) during movements [35]. It is also likely that the damping function is not as simple as the one used in the model [36], [37]. Nevertheless predictions about movement direction can be made based on the isometric force pattern and simple Newtonian mechanics.

We did not find evidence to corroborate the suggestion that the force patterns measured under isometric conditions would not be representative of the forces acting at the endpoint during actual movements. It is likely that force amplitude may be modified during actual movements, but our results suggest that the patterns of force acting at the endpoint are preserved during motion. While isometric measurements have limitations and do not necessarily represent the actual forces at the limb during movement, the inverse problem of inferring forces from movement vectors is ill-posed and often without a unique solution. Since the relationship between movement vectors during co-stimulation cannot be used to predict the relationship between the force vectors responsible for those movements, it is difficult to compare our results to those of [38].

The movements produced with sequential activation of flexor and extensor sites typically reproduced the range of vertical motion used during locomotion, but had a much smaller horizontal extent than the horizontal motion occurring during a step in an average size cat. The peak paw tangential velocity reached during movements produced with intraspinal microstimulation was about half of that obtained during swing in treadmill walking, and the overall duration of the movement was significantly longer than the typical step cycle, although the later is dependent on the timing of the stimulation cycle that we selected. These results predict that locomotor movement produced with intraspinal microstimulation would tend to be significantly slower than the cat's typical walking speed, and the steps produced would be relatively short. However, the sensory feedback is quite different in the two cases, and it is not clear what movements would be produced by intraspinal stimulation during body weight support stepping. Larger movements have been reported with intraspinal microstimulation, typically at higher stimulus intensities (up to 500 μ A and 300 μ s pulse duration [12], [39]), and these levels may be necessary to generate movement amplitudes and velocities akin to locomotion. With the stimulation parameters used and the stimulation sites used, we did not obtain bouts of locomotion. In contrast, stimulating in dorsal columns from L3 to L7 (pulse amplitude 10–90 μ A, 50–500 ms train at 70–500 Hz) generated locomotion [14]. The evoked locomotor movements were sufficient to support the cat's hindquarters on a treadmill at a relatively slow speed of 0.2 m/s. Locomotion was also obtained with long trains (10–40 s) of low amplitude stimuli delivered into the ventral grey regions of the L7–S1 spinal cord [15]. The induced locomotion had a period of about 1 s, adapted to treadmill speed (0.1–0.4 m/s), and produced plantar weight-bearing steps. For stimulation in the dorsal and intermediate zones of the L6–L7 lumbar segments, we never obtained locomotor-like movements. The responses were always of a single phase, i.e., either flexion or extension, even with stimulus train as long as 6 s. For clinical applications, activation of the locomotor generator network with intraspinal microstimulation or epidural stimulation [40], [41] may be more efficacious than constructing movements via sequential activation of spinal sites producing a single-phase response as we used in this study. Activation of single-phase responses may still be beneficial for standing or other functional activities such as stair climbing or overground obstacle avoidance. Physiologically, the evidence in the frog suggest that both co-activation and sequential activation of individual force patterns (modules or primitives) are used during reflex wiping movement [20].

Our results suggest that linear summation of individual force vectors during co-stimulation of individual sites does not occur in decerebrated spinal intact animals, and thus sequential activation of spinal sites may be preferable to co-activation of sites to create varying movement patterns in these conditions. Our evidence also strongly suggests that the forces' orientations are maintained during movements and that the endpoint movements align with the isometric force pattern.

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Fig. 1.

Reconstruction of the endpoint force pattern from measurement of isometric force vectors at the foot. Left: With the pelvis fixed, the paw was moved on a 6×6 cm grid where the dots indicate the spatial locations where forces at the paw were recorded. Right: Measured force vectors (thick dark arrows), triangles dividing the workspace, and the interpolated force vectors (thin light arrows). Forces represented are the active forces for the most common response obtained, i.e., a caudal flexion that would move the leg backward and up. The x and y position of a vector corresponds to the horizontal (x) and vertical (y) position of the endpoint of the limb, the length of each arrow corresponds to the force magnitude, and the direction of each arrow corresponds to the direction of the endpoint force.

Fig. 2.

Cluster centers of the three types of active force patterns evoked at the endpoint of the hindlimb by intraspinal microstimulation or single muscle stimulation. Left: force patterns evoked via intraspinal microstimulation: caudal flexor, caudal extensor, and rostral extensor. Right: force patterns evoked via single muscle activation of the *medial gastrocnemius* (MG), *tibialis anterior* (TA), *biceps femoris posterior* (BFP), or *vastus lateralis* (VL). The MG and BFP muscles produced CE responses, the VL produced RE responses, and the TA produced CF responses, although the TAs produced responses that were more straight up than caudally oriented. Note how the CF response for the muscle stimulation is not as caudally oriented as with intraspinal microstimulation.

Fig. 3.

Force patterns evoked by individual stimulation of two spinal sites (F_A , F_B), co-stimulation of the two sites (F_{AB}), and the best-fit force patterns of each of the three field combination models. Each panel shows the pattern of endpoint force vectors over the workspace of the limb. A scaled version of the ipsilateral response reproduced well the actual co-stimulation response, indicating that a winner-take-all interaction occurred between the two sites. The linear summation model was significantly different from the actual co-stimulation response, and in the weighted sum model the scaling factor of the contralateral response was very low, indicating the small contribution of this site to the co-stimulation response.

Fig. 4.

Movements produced via sequential activation of two spinal sites. One site produced a caudal flexor response, while the other site produced a rostral extensor response. Each site was activated for 3 s, with the two sites simultaneously activated for 0.5 s. The top panel shows the movements produced by first activating the flexor or extensor response, followed by activation of the second site. The blue line is for the movement created by the flexor then extensor sequence while the red line is for the movement using the extensor then flexor sequence. The arrows indicate the background force provided by the robot to hold the limb in a midstance position. The limb could be brought into a more caudal position by activating the flexor response first, while a more rostral position in flexion could be reached by activating the flexor with the limb in a more extended position brought upon by the activation of the extensor response. Note how the limb springs back into flexion when the extensor force pattern is turned off (blue) due to the force applied by the robot. Similarly note how the limb falls back towards its resting position when the flexor force pattern is turned off (red). B) Two movements relative to the motion of the metatarsophalangeal joint for a normal cat walking at 0.4 m/s on a treadmill. While the vertical motion of the movements produced by intraspinal microstimulation cover the range used in locomotion, the horizontal range of movement is limited compared to the one used in locomotion. A) Movements elicited with sequential activation of two spinal sites. B) Movements compared to normal step.

Fig. 5.

Tangential velocities for the movements shown in Fig. 4. Velocity was obtained by differentiation and smoothing of the endpoint position for the movements produced by stimulation, and via differentiation and smoothing of the metatarsophalangeal joint location for the cat walking on a treadmill belt. Peak velocity obtained with intraspinal microstimulation was about half of that obtained during the swing phase of gait (peak in velocity from baseline of ≈ 0.4 m/s during the stance phase). While the duration of the step was significantly shorter than the duration of the whole motion with stimulation, the duration of the movement bursts, i.e., flexion or extension at onset of stimulation compared with swing phase for walking, were of similar duration (≈ 400 ms).

Fig. 6.

A) Total isometric force pattern measured for one spinal site, and actual movement of the paw (solid line) obtained against the planar robot acting as a 100 N/m spring centered at the X with intraspinal stimulation of that site. The movement of the paw produced by forward dynamic integration of a scaled version of the isometric active forces acting at the paw for a three-link planar model of the cat hindlimb. Model and actual movements are in the same direction and proceed on a similar time course (B top). Velocity profiles of the two movements (model and actual) show higher velocity for the model, but earlier onset of movement in the actual motion (B bottom). A) Total force and actual+model motions against 100 N/m spring. B) Motion and velocity *versus* time for movement in A.

TABLE I

Relative Frequencies of Endpoint Force Field Types by Stimulation Side (Three-Link System)

field type				
stim side	Caudal Flexion	Rostral Flexion	Caudal Extension	Rostral Extension
ipsilateral	80% (16/20)	0% (0/20)	15% (3/20)	5% (1/20)
contralateral	0% (0/7)	0% (0/7)	0% (0/7)	100% (7/7)
total	59% (16/27)	0% (0/27)	11% (3/27)	30% (8/27)

TABLE II

Relative Frequencies of Endpoint Force Field Types by Stimulation Side (Two-Link System) (From [16])

field type				
stim side	Caudal Flexion	Rostral Flexion	Caudal Extension	Rostral Extension
ipsilateral	61% (31/51)	2% (1/51)	31% (16/51)	6% (3/51)
contralateral	25% (4/16)	37.5% (6/16)	37.5% (6/16)	0% (0/16)
total	52% (35/67)	10% (7/67)	33% (22/67)	5% (3/67)