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RESEARCH ARTICLE | *Control of Movement*

The role of intersegmental dynamics in coordination of the forelimb joints during unperturbed and perturbed skilled locomotion

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Zubair HN, Stout EE, Dounskaia N, Beloozerova IN. The role of intersegmental dynamics in coordination of the forelimb joints during unperturbed and perturbed skilled locomotion. *J Neurophysiol* 120: 1547–1557, 2018. First published July 11, 2018; doi:10.1152/jn.00324.2018.—Joint coordination during locomotion and how this coordination changes in response to perturbations remains poorly understood. We investigated coordination among forelimb joints during the swing phase of skilled locomotion in the cat. While cats walked on a horizontal ladder, one of the cross-pieces moved before the cat reached it, requiring the cat to alter step size. Direction and timing of the cross-piece displacement were manipulated. We found that the paw was transported in space through body translation and shoulder and elbow rotations, whereas the wrist provided paw orientation required to step on cross-pieces. Kinetic analysis revealed a consistent joint control pattern in all conditions. Although passive interaction and gravitational torques were the main sources of shoulder and elbow motions for most of the movement time, shoulder muscle torque influenced movement of the entire limb at the end of the swing phase, accelerating the shoulder and causing interaction torque that determined elbow motion. At the wrist, muscle and passive torques predominantly compensated for each other. In all perturbed conditions, although all joints and the body slightly contributed to changes in the step length throughout the entire movement, the major adjustment was produced by the shoulder at the movement end. We conclude that joint coordination during the swing phase is produced mainly passively, by exploiting gravity and the limb's intersegmental dynamics, which may simplify the neural control of locomotion. The use of shoulder musculature at the movement end enables flexible responses to environmental disturbances.

NEW & NOTEWORTHY This is the first study to investigate joint control during the swing phase of skilled, accuracy-dependent locomotion in the cat and how this control is altered to adapt to known and unexpected perturbations. We demonstrate that a pattern of joint control that exploits gravitational and interaction torques is used in all conditions and that movement modifications are produced mainly by shoulder muscle torque during the last portion of the movement.

adaptation to perturbations; cat; joint control strategy; motor control; multi-joint

INTRODUCTION

Understanding the neural control of locomotion is important, as it is necessary for the development of effective interventions in locomotion pathologies. In a number of our previous studies, we approached the neural control of locomotion by recording the activity of single neurons in chronically implanted cats. One of our recent findings was that the activity of neurons with receptive fields associated with either the shoulder, elbow, or wrist differs in pattern and, occasionally, in intensity (Beloozerova et al. 2013). The joint-related differences were found for neurons of the motor cortex that project to the pyramidal tract (Stout and Beloozerova 2012), neurons of the ventrolateral thalamus projecting to the motor cortex (Marlinski et al. 2012a), and neurons of the reticular nucleus of the thalamus (Marlinski and Beloozerova 2014; Marlinski et al. 2012b). As discussed by Beloozerova et al. (2013), the results of these studies suggest that during locomotion, the thalamo-cortical network processes information about motion and generates control differently at the shoulder, elbow, and wrist.

Distinct control of different joints during multi-joint movements was also suggested by studies of arm movements that used kinetic analysis of joint dynamics (Dounskaia et al. 1998; Galloway and Koshland 2002; Hirashima et al. 2003). These and other studies revealed differences across the joints in the role of muscle torque that represents active control of each joint. It was found that one ("leading") joint is usually rotated by muscle torque, whereas passive interaction torque caused by mechanical interactions among limb segments plays a major role in rotation of the other ("trailing") joints (for reviews, see Dounskaia 2010 and Dounskaia and Shimansky 2016). It was also shown that if the task can be performed through different movements, there is a tendency to perform the movements during which the contribution of muscle torque in the production of trailing joint motions is decreased, and thus, the role of interaction torque at these joints is maximized (Dounskaia and Goble 2011; Goble et al. 2007). When movements are not horizontal, and gravitational torque affects joint rotations, there is a tendency to use gravitation for joint rotation (Wang and Dounskaia 2016). At the leading joint, gravitational torque can be used instead of muscle torque to generate motion. At the trailing joints, gravitational torque can be used to assist interaction torque in passive rotation of the joint.

In most cases, the leading role is played by the proximal joints, and the distal joints trail. Therefore, the differences in control of the leading and trailing joints can be partially explained by differences in biomechanical properties of proximal and distal limb segments. Interaction torque caused at the

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proximal joint by rotation of the distal joints is small relative to torque generated by muscles spanning the proximal joint. In contrast, interaction torque exerted at the distal joint is large relative to muscle torque. However, a strategic nature of the joint control differences is evident from findings such as the tendency to maximize the contribution of passive torques to motion production at the distal joints in normal, especially skilled movements and increased contribution of muscle torque at the distal joints in motor disorders (for review, see Dounskaia and Shimansky 2016). These considerations prompted a hypothesis that the brain exploits the biomechanical properties of multi-articular limbs to produce limb movements and uses the proximal joint to generate interaction torque, which, together with gravitational torques, plays the cardinal role in the production of the distal joint motion required by the task (Dounskaia 2005; Dounskaia and Shimansky 2016). The role of distal musculature is to regulate passive joint motion and adjust it to task requirements. We refer to this pattern of joint coordination as a "trailing" joint control pattern.

Although ample support for the use of the trailing joint control pattern has been obtained for upper extremity movements, whether this pattern is used for control of lower extremity movements during locomotion remains unknown. Although influence of passive torques on joint motion has been demonstrated for locomotion in humans (McFadyen and Winter 1991; Patla and Prentice 1995; Ulrich et al. 1994; Zernicke et al. 1991) and cats (Hoy and Zernicke 1985, 1986; McFadyen et al. 1999; Prilutsky et al. 2005; Wisleder et al. 1990), whether the coordination of the lower extremity joints follows the trailing pattern remains unknown. Uncovering this pattern would be informative with respect to the control strategy applied to the limbs during locomotion and may help to understand differences in neuronal activity across the joints revealed in cats (Beloozerova et al. 2013). Accordingly, the first goal of the present study was to examine whether the trailing pattern of control of the shoulder, elbow, and wrist of the cat's forelimb is observed during the swing phase of locomotion. The forelimb was used because the majority of the studies of neuronal activity during locomotion in cat focused on the forelimb (Beloozerova et al. 2013).

Another gap in the research of multi-joint movement control is a lack of understanding of joint control during movement corrections in response to perturbations. The trailing joint control pattern was revealed for unperturbed movements only. This pattern predicts that the leading joint, the role of which is to generate energy for the entire limb movement, is controlled predominantly in a feedforward manner based on the general characteristics of the required movement, such as speed and amplitude (Dounskaia 2005). Some adjustments of the distal joint motions are also planned in advance, at least grossly, in anticipation of the effect of interaction and gravitational torques (Goble et al. 2007; Sainburg et al. 1999). It remains unclear how control of the proximal (leading) and distal (trailing) joints is influenced by feedback about changes in the environment that require quick adjustments of joint motions. On the one hand, the distal joints may play the major role in feedback-based adjustments because the role of the trailing joint musculature is to regulate passive motion of these joints and adjust it to task requirements. On the other hand, the leading joint may be used to produce fast changes in interaction torque at the trailing joints, which would result in adjustments of the entire limb motion. Therefore, the second goal of the present study was to examine changes in joint control within the cat's forelimb when expected and unexpected adjustments to the limb motion were required.

To pursue the two goals, we investigated joint control in the forelimb as cats walked along a raised horizontal ladder that required accurate foot placement. One of the cross-pieces was motorized and could be displaced either toward or away from the cat before the cat stepped on it. The trials in which the motorized cross-piece remained stationary were used to study the general structure of joint control during cat locomotion with accurate foot placement. Displacements of the motorized cross-piece and manipulations of the direction and timing of these displacements were used to study adjustments in joint control in response to changes in the environment.

METHODS

Recordings were obtained from three adult male cats with weights of 5 (*cat 1*), 4 (*cat 2*), and 3.5 kg (*cat 3*). *Cats 1* and *2* were middle age; their exact age is unknown; *cat 3* was 1 yr old. Methods of data collection were reported in our previous studies (Beloozerova et al. 2010; Stout et al. 2015a), and therefore, they are described here only briefly. All experiments were conducted in accordance with National Institutes of Health (NIH) guidelines and with the approval of the Barrow Neurological Institute Animal Care and Use Committee.

Data from *cats 1* and *2* used here were also used in two previous studies of locomotion mechanics (Klishko et al. 2014; Stout et al. 2015a). Before participating in the present study, *cats 1* and *2* underwent a head implant surgery and were used in studies of the activity of motor cortex and motor thalamus during locomotion, the results of which were reported by Beloozerova et al. (2010), Stout et al. (2015a), and Marlinski et al. (2012a, 2012b). *Cat 3* did not contribute to any studies except the present study, and no surgeries were performed on *cat 3*.

Locomotion tasks. Positive reinforcement (food) was used to adapt cats to the experimental environment and to engage them in locomotion. All training and recording sessions were conducted under normal room illumination. A closed walkway consisting of two connected corridors served as an experimental chamber. In each corridor, the walkway was 2.5 m long and 0.3 m wide. Cats passed repeatedly around the chamber in the counterclockwise direction. The passage of the cat through the beginning and end of each corridor was monitored using infrared photodiodes. In one of the corridors the floor was flat, whereas the other corridor contained the horizontal ladder with 10 cross-pieces (Fig. 1). Cross-pieces were spaced 25 cm apart, which is approximately half of the mean step length observed in the chamber

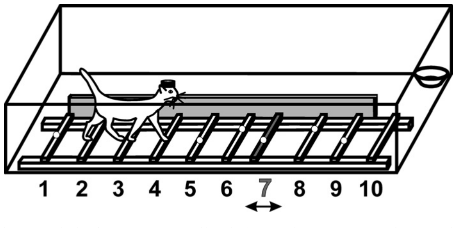

Fig. 1. Experimental design. Cats walked through a rectangular, 2-sided chamber. One side contained a raised horizontal ladder, with 1 motorized cross-piece (no. 7, gray) that was displaced at different times as the cat walked in the chamber. A total of 7 conditions were analyzed: an unperturbed condition with the cross-piece remaining in its central position, when all cross-pieces were equally spaced 25 cm apart, and 6 conditions representing combinations of 2 directions (toward and away from the cat) and 3 latencies ("known", "unknown long", and "unknown short"; see the text for explanations) of displacements of the motorized cross-piece.

during locomotion on flat floor at a self-selected pace (Beloozerova et al. 2010; Beloozerova and Sirota 1993). The tops of the cross-pieces were flat and 5 cm wide. This width was chosen to slightly exceed the cat's mean foot length (3 cm) so that cats could have full foot support on a cross-piece. Cross-pieces were elevated 6 cm above the floor of the chamber. One cross-piece (the 7th from the left side of the ladder; Fig. 1) was connected to an electric motor. When displaced, it was shifted 5 cm in either direction, such that there was no overlap between the cross-piece position before and after the displacement. Displacement was completed within 145 ms of initiation. There was a yellow light-emitting diode (LED) lamp on the side of the cross-piece facing the cat. The lamp was lit when the cross-piece displacement was initiated, regardless of the displacement direction. This illumination attracted the cat's attention to the displacing cross-piece. Auditory cues from the activation of the motor also alerted the cat to the cross-piece displacement. Regardless of the cross-piece's displacement or the cat's performance, after each round of walking, the cat received food in a feeding dish located in one of the chamber's corners.

The motorized cross-piece was displaced in two directions, toward or away from the cat, which required the cat to take a smaller or larger step, respectively. Also, the cross-piece was displaced at three different time points along the cat's progression around the chamber, which manipulated the time the cat had to adjust the length of the step. The first timing provided a "known" displacement condition, in which the cross-piece was displaced while the cat was at the feeder. In this condition, the cat did not see movement of the cross-piece, as the ladder was in its final configuration when the cat stepped onto it. The cat had two full strides of the right forelimb, a stride from *cross-piece no. 1* onto *cross-piece no. 3* and a stride from *cross-piece no. 3* onto *cross-piece no. 5*, before making a smaller or larger step to reach the displaced *cross-piece no. 7*. Here, we refer to the sum of the swing and stance locomotor phases of one limb as a "stride," and we refer to the swing phase of a stride as a "step." In the second "unexpected long-notice" timing condition, the cross-piece was displaced when the cat's right forelimb stepped on *cross-piece no. 3*. The cat had one full stride to complete before needing to adjust. In the third,"unexpected short-notice" timing condition, the cross-piece was displaced when the cat's right forelimb stepped on *cross-piece no. 5*, and the very next transfer of this limb had to be adjusted. Total, seven conditions were used: unperturbed, when the cross-piece remained in its original location; and six conditions representing the combinations of the two directions and three timing conditions of the cross-piece displacement. They were presented pseudorandomly by a computer program so that the cat could develop no foreknowledge of which condition would be presented. Only passages where the cat stepped on the displaceable cross-piece with the right forelimb were studied.

Cats were trained to wear light-emitting diodes (LEDs) on the lateral aspect of the right forelimb, which were used for motion recording, as described below. The LEDs were attached to the shaved skin covering the joints using double-sided adhesive tape. Cats were also accustomed to wearing a cotton jacket and a light backpack with connectors and preamplifiers. After training, the cats did not show any signs of discomfort when wearing these objects, and they appeared to walk normally. The task was habitual for *cats 1* and *2*, as they participated in other similar experiments before data presented here were collected, including performance of this particular locomotion task during a month-long study of the motor cortex activity (Stout et al., 2015a). *Cat 3* was trained for this specific experiment for ∼1 mo before data collection.

Motion capture and kinematic analysis. Motion of the right forelimb was recorded using the computerized, active-marker, three-dimensional, real-time motion capture and analysis system Visualeyez (VZ-4000; Phoenix Technologies). Six wide-angle LEDs were placed on the skin projections of the greater tubercle of the humerus (shoulder joint), approximate elbow joint center, ulna styloid process (wrist joint), base of the fifth metacarpals (metacarpophalangeal joints), the middle toe, and the right scapula, which was the trunk anatomica landmark. Also, each cross-piece of the ladder had a corresponding LED on the side facing the camera for monitoring progression of the cat through the ladder. Three-dimensional positions of all LEDs were recorded at 111.1 Hz sample frequency throughout the duration of the experiment. Error of measuring distances on a rigid test object was <2.3 mm. The first five LEDs were used to calculate shoulder, elbow, and wrist angles using the VZ Analyzer software. These LEDs and the definitions of the three joint angles are shown in Fig. 2*A*. According to these definitions, the positive direction of joint rotation was flexion at the shoulder and elbow and dorsiflexion at the wrist.

The obtained motion data were exported to Matlab (MathWorks, Natick, MA) and filtered using a 4th order zero-lag Butterworth filter with a cutoff frequency of 6 Hz. Only motion of the right forelimb during stepping between *cross-piece nos. 5* and *7* (as indicated by the

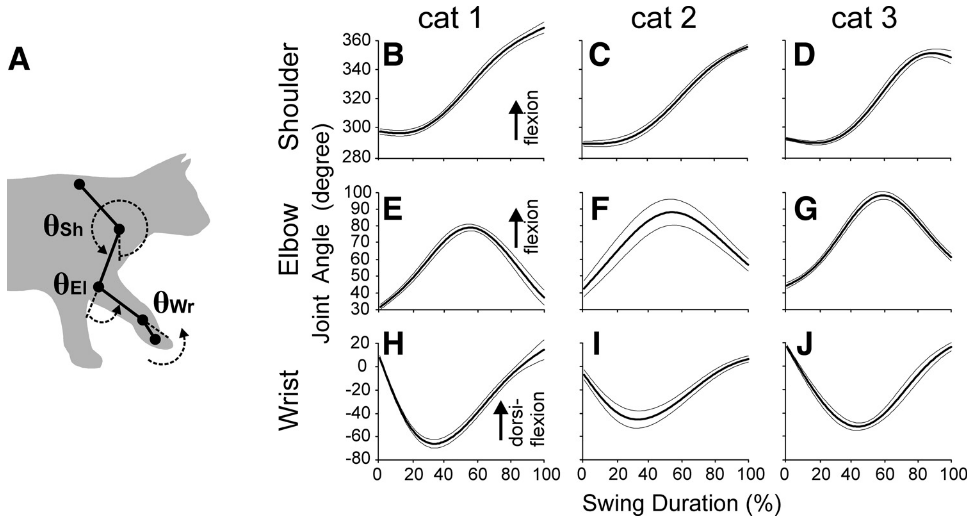

Fig. 2. Definition of angles at the shoulder, elbow, and wrist joints and joint angular displacements during the swing phase of the unperturbed step. *A*: ●, locations of the light-emitting diode (LEDs) used for joint angle calculation. The shoulder angle was defined as the counterclockwise deviation of the upper arm from the vertical. The elbow angle was defined as the angle between the upper arm and forearm. The wrist angle was defined as the counterclockwise deviation of the paw from the forearm axis. This definition resulted in positive joint rotations during flexion at the shoulder and elbow and dorsiflexion at the wrist. *B–J*: joint angle displacements during the swing phase of the unperturbed step for shoulder (*B–D*), elbow (*E–G*), and wrist (*H–J*). The thick lines show joint angles averaged at each point of normalized time across all steps in the unperturbed condition for each cat stepping onto cross-piece no. 7, and the thin lines show SD.

data from the LEDs on the cross-pieces) was analyzed. Joint angular velocities and linear velocity of the paw end point (the LED located on the middle toe) were obtained by differentiating the joint and end-point position data. The end-point velocity was computed as the magnitude of a two-dimensional vector that included the vertical and longitudinal components in the sagittal plane. The swing phase was determined as the time period during which the end-point velocity was >5% of its maximum velocity within this step. The majority of swing phases performed by each cat in each condition had similar durations. We selected swing phases in each condition that did not differ by >20 ms in duration. As a result, six to 15 steps were selected for analysis in each of the seven conditions for each cat. Durations of the selected swing phases were normalized to yield 100 data points in each movement. Characteristics computed for each movement were averaged across the selected swing phases in each condition for each cat.

Parameters of the forelimb segments, including forelimb segment lengths, masses, centers of mass, and moments of inertia were estimated according to regressive relationships presented by Hoy and Zernicke (1985). The parameters are shown in Table 1 for each cat. The paw segment was defined as a combination of the carpals and digits. The segment parameters were used to compute torques at each joint, as described in *Kinetic analysis*. The segment lengths were also used to compute contributions of motion of the body and three joints to the end-point velocity according to a method presented in the APPENDIX. When averaged contribution of the body and each joint to the end-point velocity had to be assessed, mean values computed for normalized time did not have a physical meaning. Therefore, we integrated the contributions to the end-point velocity across the considered movement period, which yielded contributions of the body and each joint to the distance covered by the end point.

Kinetic analysis. Inverse dynamics equations adopted from Hirashima et al. (2003) were used to calculate torques at the shoulder, elbow, and wrist in the sagittal plane. Four torques were calculated at each joint: net torque (NT), interaction torque (IT), gravity torque (GT), and muscle torque (MT); NT = MT + IT + GT. NT is proportional to the angular acceleration of the joint. IT is passive torque generated by mechanical interactions among the limb segments. GT is passive torque generated by gravitational force acting on limb segments. The sum of IT plus GT represents total passive torque (PT) acting at the joint. MT was computed as the difference, MT = NT − IT − GT. It predominantly represents active torque generated by contractions of muscles spanning the joint, although it also includes passive torque caused by elasticity of muscles and ligaments at the joint. According to the definition of the joint angles (Fig. 2*A*), torques were positive when they acted into acceleration of the shoulder and elbow into flexion and of the wrist into dorsiflexion. Note that the expression “joint acceleration into flexion” is used here to describe both acceleration of joint flexion and deceleration of joint extension. Accordingly, “joint acceleration into extension” represents either acceleration of joint extension or deceleration of joint flexion.

Table 1. *Parameters of the forelimb segments*

	Length, cm	Mass, g	Moment	Center of Mass, cm
Cat 1				
Scapula	9.0	97.9	677.4	4.29
Upper Arm	10.3	112.0	905.6	5.03
Forearm	11.0	60.7	691.1	5.00
Carpals	3.5	13.5	10.6	1.83
Digits	3.5	7.3	22.3	1.75
Cat 2				
Scapula	7.5	77.8	488.1	3.57
Upper Arm	10.0	97.2	788.2	4.88
Forearm	10.0	48.2	452.0	4.54
Carpals	3.0	9.7	7.8	1.57
Digits	3.0	6.0	13.6	1.50
Cat 3				
Scapula	6.4	68.1	394.9	3.05
Upper Arm	9.0	78.6	538.1	4.39
Forearm	9.0	42.5	326.0	4.09
Carpals	3.7	10.7	9.2	1.93
Digits	2.8	5.6	10.9	1.40

To assess the role of MT and the passive torques in generation of NT at each joint, MT contribution (MTC) to NT was computed as a mean of *MTC(i)*, which was computed using the formula (Dounskaia and Wang 2014; Lee et al. 2007)

$$MTC(i) = \begin{cases} MT(i)/NT(i), & if \;\; 0 < MT(i) < NT(i) \\ 1, & if \;\; MT(i) \geq NT(i) \\ 0, & if \;\; MT(i) < 0 \end{cases} \quad , \qquad (1)$$

where $i = 1,...,n$ is a moment of time within the considered movement period and n is the number of data points within that period. Computed in this way, MTC is constrained between 0 and 1. Values close to 1.0 signify that NT at the joint was produced largely by MT, whereas PT resisted NT and was suppressed by MT. Accordingly, MTC values near 0.0 signify that NT was generated primarily by PT and that MT was smaller in magnitude and opposite in sign. Thus, MTC shows whether the joint was rotated predominantly by MT or by PT during the considered movement period.

To study how each passive torque, IT and GT, contributed to joint rotation, the analysis of MTC was complemented with analysis of signed impulses of MT, IT, and GT (Dounskaia et al. 2002; Sainburg and Kalakanis 2000). Namely, the signed impulse of a torque was computed over a period of time as a sum of absolute torque values taken with the positive sign if the torque coincided in sign with NT and with the negative sign if the torque was opposite in sign to NT at that time moment.

The computed kinematic and kinetic characteristics obtained in the unperturbed condition were used to examine the organization of joint control during forelimb swing. The characteristics obtained in the six cross-piece displacement conditions were used to assess the effects of the displacement direction and timing on joint control. Namely, a two-way 2 × 3 (direction × timing) ANOVA with repeated measures was applied to MTC and contributions of the body and three joints to end-point velocity. These data were computed for each of the three cats as an average across all trials selected for analysis for that cat in each condition. The significance level was set at 0.05. When a significant timing effect was found, post hoc multiple comparisons were conducted using the Bonferroni test, which adjusted the observed significance level to 0.05, with the use of $P = 0.016$ for pairwise comparisons.

RESULTS

The average duration of the swing phase of unperturbed steps was 253, 231, and 250 ms in *cats 1*, *2*, and *3*, respectively. The swing duration was 9–11 ms shorter during the small steps and 18–19 ms longer during the large steps in each cat.

Joint movements were similar across the three cats. This is observed in Fig. 2, *B–J*, which shows averaged joint displacements during the swing phase of the unperturbed step obtained from each cat. In all cats, the shoulder initially produced little motion and then flexed starting from the middle of the swing phase. The elbow initially flexed and then extended, whereas the wrist initially plantarflexed and then dorsiflexed. This pattern of joint motions during the swing phase is similar to that previously reported by Prilutsky et al. (2005).

Contributions of joint motions to end-point velocity in the unperturbed condition. A representative example of the contributions of joint motions to the limb end-point velocity during the swing phase of unperturbed steps performed by *cat 2* are shown in Fig. 3*A*. The end point accelerated in the direction of motion during the early portion of the swing phase, attaining the maximal speed at ~20% into the swing phase, held this speed for about half of the cycle, and decelerated during the final 30% of the swing phase. The contribution to this velocity from the body translation was roughly consistent throughout the entire swing phase. Increases and decreases in the end-point velocity were due primarily to the rotation of the forelimb joints. During the first 40% of the swing phase, the elbow joint rotation was responsible primarily for propelling the paw in the direction of motion, whereas shoulder joint rotation had little contribution, and wrist rotation had a negative effect. At 40% into the swing phase, these roles were switched; during the rest of the swing, the shoulder joint rotation produced much of the end-point velocity whereas joint velocity contribution was small at the wrist and negative at the elbow.

Joint control during unperturbed steps. Data from *cat 2* were again used to give an example of profiles of NT and its components MT, IT, and GT (NT = MT + IT + GT) at the three joints obtained as an average across all unperturbed steps (Fig. 3, *B–D*). Shoulder NT was positive during the first 60% of the swing phase and negative during the rest of the movement (Fig. 3*B*). The positive portion of shoulder NT was generated predominantly by GT and IT, although MT was also positive at the very beginning of the movement. The negative portion of shoulder NT was caused exclusively by MT, with IT being slightly resistive and GT being near zero. NT for the elbow was positive during the first and last 20% of the movement, and it remained negative in the middle of the movement (Fig. 3*C*). The initial positive values of NT were produced mainly by MT, with IT being strongly resistive. During the rest of the movement, elbow NT was produced passively, predominantly by IT, with MT being resistive. Wrist NT mainly followed the sign of GT, whereas IT and MT compensated for one another (Fig. 3*D*). All wrist torques were low in the middle of the movement period, and therefore, the role of MT in the wrist movement production was largely limited to the first 20 and last 40% of the movement.

The qualitative observations from the torque profiles in Fig. 3 obtained from a single cat were verified for all cats by computation of MTC and MT, IT, and GT impulses, which clarified the contribution of each torque to NT and thus to joint acceleration. Because Fig. 3 revealed changes in joint control throughout the movement, these characteristics were computed separately for the four quarters of movement time: 0–25, 26–50, 51−75, and 76–100%. The division into movement quarters was chosen because shoulder and elbow NT changed in sign close to the 25 and 75% of movement time. Figure 4 shows the results averaged across the three cats. During the first quarter of the movement, MTC was below 0.5 at the shoulder and near 1 at the elbow. This indicates that shoulder NT was produced predominantly by the passive torques, and elbow NT was produced mainly by MT. The torque impulses confirm this conclusion, showing that, at the shoulder, the major contributor to NT was GT, although MT assisted motion. At the elbow, GT impulse was small and IT impulse negative, and only MT impulse was positive and substantial. In the second quarter, low MTC indicates that both joints moved largely passively, and the torque impulses specify that both IT and GT contributed to shoulder NT, and IT was the major contributor to elbow NT. In the third and fourth quarters, shoulder NT was generated predominantly actively by MT, and elbow NT was produced passively by both IT and GT in the third quarter and mainly by IT in the fourth quarter. At the wrist, MT and GT contributed to NT about equally in the first quarter, the joint was rotated largely passively in the second and third quarters with MT dampening the effect of the passive torques, and substantial MT impulse was generated to counteract high IT in the last quarter.

Compared across the joints, these results show that when the shoulder or elbow was accelerated mainly by MT (the elbow at the movement beginning and the shoulder at the movement end), the other joint was accelerated predominantly passively. Both joints were accelerated predominantly passively in the middle of the movement.

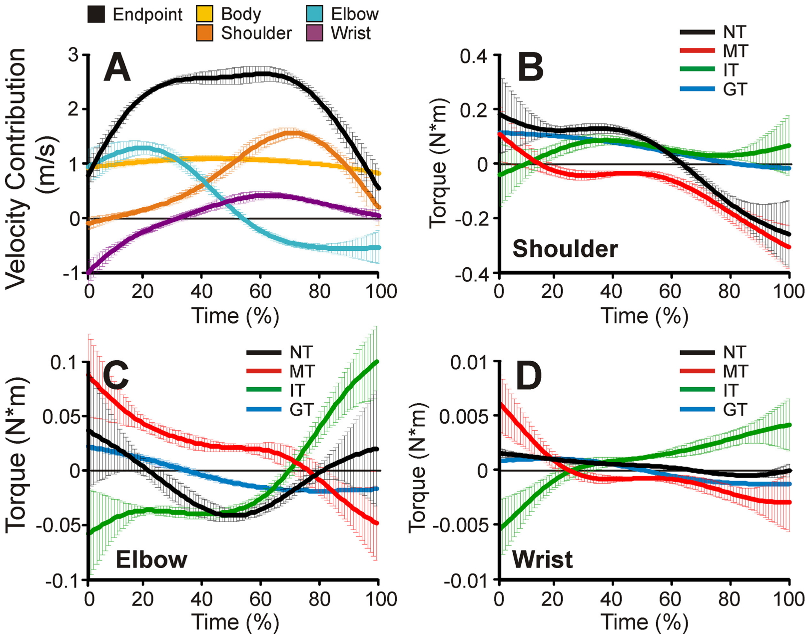

Fig. 3. A representative example of profiles of joint motion contributions to the end-point velocity (*A*) and net (NT), muscle (MT), interaction (IT), and gravity torque (GT) at the shoulder (*B*), elbow (*C*), and wrist (*D*) during the swing phase of unperturbed steps of *cat 2*. Positive values of the torques signify that they acted to accelerate the joint into flexion at the shoulder and elbow and into dorsiflexion at the wrist.

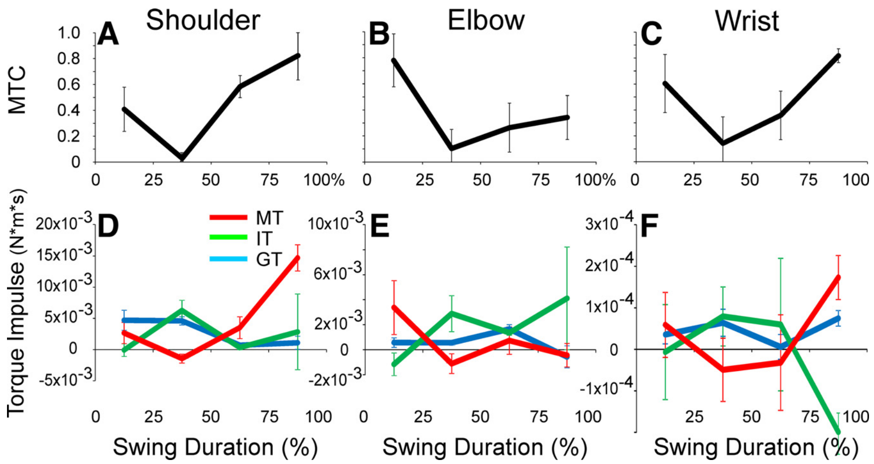

Fig. 4. Muscle torque contribution (MTC) and impulses of muscle (MT), interaction (IT), and gravity torque (GT) at the shoulder, elbow, and wrist joints during each quarter of the swing movement in the control condition averaged across all cats. The error bars represent SD.

Changes in joint contributions to end-point motion during perturbed steps. To assess changes in the contributions of the body, shoulder, elbow, and wrist to the end-point motion in the six perturbed conditions, we integrated these contributions within each movement quarter. The resultant contributions of each body part to the distance covered by the end point are shown in Fig. 5. For each body part, this contribution shortened during small steps (when the cross-piece shifted toward the cat) and lengthened during large steps (when the cross-piece shifted away from the cat). A significant main effect of direction revealed by a two-way 2 × 3 (direction × timing) ANOVA indicated that this difference between the small and large steps was significant for the body in all four movement quarters [$F_{(1,2)} = 1{,}569$, $P < 0.001$, $\eta^2 = 0.99$; $F_{(1,2)} = 107$, $P < 0.01$, $\eta^2 = 0.98$; $F_{(1,2)} = 35$, $P < 0.03$, $\eta^2 = 0.94$; and $F_{(1,2)} = 25$, $P < 0.04$, $\eta^2 = 0.93$ for *quarters 1– 4*, respectively] and for the shoulder in *quarters 2*, *3*, and *4* [$F_{(1,2)} = 20$, $P < 0.05$, $\eta^2 = 0.91$; $F_{(1,2)} = 48$, $P = 0.02$, $\eta^2 = 0.96$; and $F_{(1,2)} = 42$, $P < 0.03$, $\eta^2 = 0.95$, respectively]. The main effect of direction approached significance at the elbow in *quarter 2* [$F_{(2,1)} = 15$, $P = 0.061$, $\eta^2 = 0.88$] and was significant in *quarter 3* [$F_{(2,1)} = 19$, $P = 0.05$, $\eta^2 = 0.90$]. At the wrist, the main effect of direction was significant only in *quarter 1* [$F_{(2,1)} = 79$, $P < 0.02$, $\eta^2 = 0.97$].

These results show that the adjustments of the step length were done predominantly by the body and shoulder, and the contribution of the elbow and wrist to motion adjustments was small. Also, Fig. 5 shows that the major adjustments of the step length were produced by the shoulder at the end of the movement. When the cross-piece shifted toward the cat, the shoulder shortened the step on average across the three timing conditions by 1.68 cm in *phase 3* and 2.76 cm in *phase 4* for a total of 4.44 cm. When the cross-piece shifted away from the cat, the shoulder lengthened the step on average by 0.77 cm in *phase 3* and 3.1 cm in *phase 4* for a total of 3.87 cm. Because

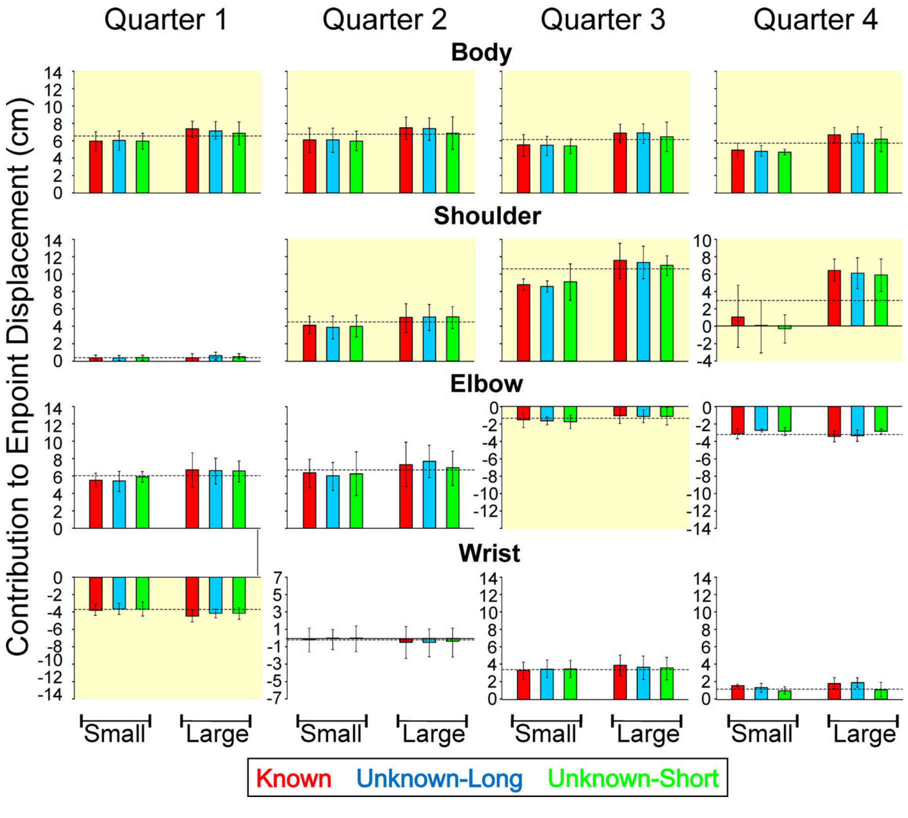

Fig. 5. Effect of the direction and timing of the cross-piece displacement on the contributions of the body, shoulder, elbow, and wrist to distance covered by the paw in each quarter of the swing phase of perturbed steps. In all graphs, the horizontal dashed line indicates the contribution during unperturbed steps. Here and in Fig. 6, mean values for all 3 cats are shown. The error bars show SD. Yellow background indicates a significant difference between small and large steps. The labels “small” and “large” indicate changes in the step size when the cross-piece was shifted toward and away from the cat, respectively. The labels “unknown long” and “unknown short” represent the unknown long-notice and short-notice perturbations, respectively.

the cross-spiece shifted for 5 cm in each condition, these numbers show that the shoulder motion in *quarters 3* and *4* accounts for ~80% of the adjustments in the step length.

The only significant main effect of the timing of the cross-piece displacement was for the body in *quarter 4* [$F_{(2,4)} = 13$, $P < 0.02$, $\eta^2 = 0.87$]. Post hoc testing did not reveal any differences among the three timing conditions. However, Fig. 5 suggests that the body contribution in *quarter 4* decreased in the unknown short-notice condition. This decrease was especially noticeable for the large steps. The only significant interaction was for the wrist in quarter 3 [$F_{(2,4)} = 10$, $P < 0.03$, $\eta^2 = 0.83$]. Figure 5 clarifies that the wrist contribution decreased slightly with shortening of the notice timing, but only during large steps.

Changes in joint control during perturbed steps. Figure 6 shows MTC in the six perturbed conditions. The two-way 2 × 3 (direction × timing) ANOVA did not reveal any significant main effects at the shoulder, although the interaction was significant in *quarter 4* [$F_{(2,4)} = 26$, $P < 0.01$, $\eta^2 = 0.93$]. Figure 6 clarifies that shoulder MTC decreased with shortening of the time available for the adjustment, but only during large steps. Similarly, a significant interaction at the elbow in quarter 4 [$F_{(2,4)} = 14$, $P < 0.02$, $\eta^2 = 0.88$] pointed to a decrease in elbow MTC with shortening of the time available for the step adjustment but only for large steps. Additionally, the main effect of timing was significant at the elbow in *quarter 1* MTC [$F_{(2,4)} = 20$, $P < 0.01$, $\eta^2 = 0.91$]. Although post hoc testing did not reveal any significant differences between the three timing conditions, Fig. 6 suggests that the elbow MTC decreased in the short-notice condition, particularly for large steps. At the wrist, the only significant effect was an interaction in *quarter 4* [$F_{(2,4)} = 14$, $P < 0.02$, $\eta^2 = 0.87$]. Figure 6 shows that wrist MTC increased in the short-notice condition during the small step and in both unexpected perturbation conditions during the large step.

To summarize, the effect of direction and timing of the cross-piece displacements on MTC was limited and observed at the three joints mostly during the last quarter of the movement, when displacements were unexpected and required a longer step.

DISCUSSION

The importance of understanding how joint coordination is organized during movements of multi-articular limbs with redundant degrees of freedom was emphasized by Bernstein (1967). Understanding locomotor movements is particularly important, not only because it is one of the most common behaviors observed in humans and animals but also because these movements must be highly adaptable to overcome the complex and changing constraints posed by natural environments. Unperturbed locomotion over a raised horizontal ladder is itself a complex task that requires precise foot placement. Locomotion over such complex terrain requires the involvement of supraspinal centers such as the motor cortex (Beloozerova and Sirota 1993; Chambers and Liu 1957; Friel at al. 2007; Liddell and Phillips 1944; Trendelenburg 1911). The present study is the first to investigate coordination of the forelimb joints in cats during the swing phase of a complex, skilled locomotion task and how the joint control is altered in response to known and unexpected perturbations.

Forelimb joint control during the swing phase of unperturbed steps. The contribution of joint motions to end-point velocity was produced initially by the elbow and then by the shoulder while the contribution of wrist motion was low. The minor contribution of the wrist despite substantial angular displacement at this joint (Fig. 2) suggests that the role in the production of the limb movement differed between the wrist and two proximal joints. Namely, the shoulder and elbow were used to transport the paw in space. In contrast, the wrist was likely responsible for providing the orientation of the paw required to clear off the previous cross-piece and prepare for stepping on the next cross-piece.

Kinetic analysis revealed that the movement consisted of three periods characterized by distinct patterns of shoulder and elbow coordination. During the first period, MT played a major role in accelerating the elbow while the shoulder was acceler-

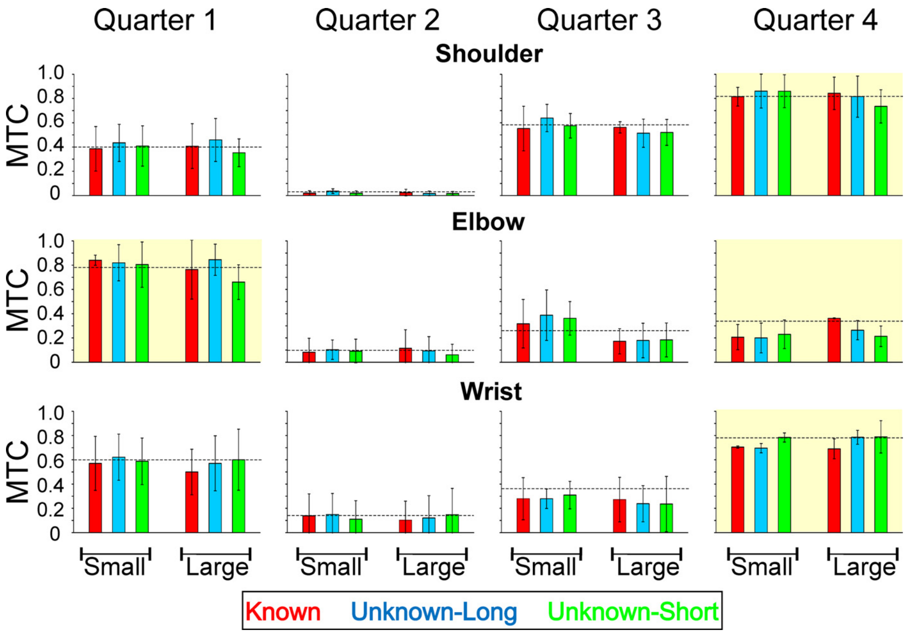

Fig. 6. Effect of the direction and timing of the cross-piece displacement on the muscle torque contribution (MTC) at the shoulder, elbow, and wrist joints within each quarter of the swing phase of perturbed steps. In each graph, the horizontal dashed line indicates the mean MTC during unperturbed steps.

ated predominantly passively due to GT, with MT first assisting and then resisting shoulder acceleration. During the second period, both joints were accelerated by passive torques, with MT being low and dampening joint acceleration. During the third period, shoulder MT took the lead, accelerating this joint and generating IT that determined the direction of elbow acceleration. At the wrist, the role of MT was largely to cope with large IT caused by motion of the two proximal joints at the movement beginning and end. These observations are consistent with joint control reported in previous studies during the swing phase of the hindlimb in different types of cat locomotion (Hoy and Zernicke 1985; Prilutsky et al. 2011; Smith et al. 1993), except that the knee was usually accelerated by passive torques throughout the entire movement. An exception was trot in Smith et al. (1993) that also demonstrated active control of the knee at the very beginning of the swing phase.

The organization of control during which one joint is rotated predominantly actively (MTC > 0.5) and the other largely passively (MTC < 0.5) has been documented in a variety of skillful movements of the human arm (Ambike and Schmiedeler 2013; Dounskaia et al. 2002; 1998; Galloway and Koshland 2002; Graham et al. 2003; Hirashima et al. 2003), and it has been addressed as a trailing joint control pattern (see Dounskaia and Shimansky 2016 for review). It was hypothesized that the trailing pattern represents a control strategy during which one ("leading") joint generates energy for motion of the entire arm, like a handle that brings in motion the entire whip. The leading joint is accelerated/decelerated by the musculature spanning this joint, and it generates IT that, together with GT, becomes the major cause of motion at the other ("trailing" or "subordinate") joint (Dounskaia 2010; 2005). The musculature at the trailing joint provides regulation of passive motion of this joint with respect to the leading joint motion, assisting or resisting motion, depending on the task requirements (Kim et al. 2009).

The shoulder and elbow joint control during the swing phase revealed here is consistent with this "leading joint" hypothesis. The elbow served as the leading joint and the shoulder as a trailing joint during the first movement period. The shoulder served as the leading joint and the elbow as a trailing joint during the third period. In between, both joints were accelerated by passive torques. Passive rotation at both joints is consistent with the leading joint control strategy because it satisfies the central aspect of this strategy, namely that passive effects are exploited for joint coordination. Wang and Dounskaia (2016) provided an example of movements during which GT played the major role in acceleration of both joints. Also, passive elasticity of periarticular tissues spanning the joint can generate a significant portion of MT, especially when motion approaches anatomic limits of joint rotation (Dounskaia et al. 1998; Simonsen et al. 2012). The use of passive effects for rotation of both joints is also consistent with an interpretation that the trailing joint control pattern minimizes the amount of information the brain needs to process for joint coordination (Dounskaia and Shimansky 2016). As discussed in that study, passive rotation of both joints satisfies this optimization criterion even better than the use of a single joint for generation of energy for the entire movement.

The wrist also was a trailing joint during the studied movement. Although MTC results show that MT dominated wrist control at the very beginning and end of the swing phase, the wrist did not generate energy for motion of the other joints, and therefore, it did not serve as a leading joint. Wrist MT was likely used to interfere with passive torques (which is typical of trailing joints), with the purpose to orient the paw in space as required for departure from the previous cross-piece and stepping on the next cross-piece.

Forelimb joint control during the swing phase of perturbed steps. The changes in the contribution of the body and joints to the step size (Fig. 5) strongly depended on the direction of the cross-piece displacement. Differences between the "small" and "large" steps were observed at the body and all joints, even in the first movement quarter, and lasted throughout the movement. This indicates that some reaction to perturbations was produced at the very beginning of the swing phase or during the preceding stance phase in all timing conditions, even in the short-notice condition. However, the major adjustments in the step size were produced by the shoulder in the third and especially fourth quarter, i.e., at the very end of the swing phase.

In contrast to the effect of the cross-piece displacement direction, the effect of the displacement timing on the contributions of the body parts to the step size was minor. There were some decreases in the contribution of the body in the fourth quarter and of the wrist in the third quarter in the short-notice condition, but only when a larger step had to be performed. The contributions of the shoulder and elbow were not influenced.

The MTC analysis showed that the organization of joint control used during corrections for perturbations in all direction and timing conditions was similar to that used in the unperturbed condition (Fig. 6). There was no significant effect of the direction of the cross-piece displacement on MTC at any joint and any movement phase. Displacement timing provided a only minor influence on MTC. Therefore, it can be concluded that the joint control strategy remained the same in all timing and direction conditions. At the shoulder and elbow, it included the three periods of control: the elbow leading and shoulder trailing, both joints trailing, and shoulder leading and elbow trailing. The leading role of the shoulder during the last movement portion accounts for the finding that the major changes in the step size in response to cross-piece displacements were produced by the shoulder at the final movement phase. Musculature of the shoulder modified motion of this joint and the entire limb.

The formulated conclusions are limited by the fact that the data were obtained from three cats only, all of which were males. However, the consistency of the results across the cats as well as across the seven tested conditions suggests that the conclusions may hold for a larger and more diverse population.

The similarity of the joint control strategy across all studied conditions points to high robustness of this strategy. It is likely that the same joint control strategy is also used during stepping on a flat surface (examined by Prilutsky et al. 2005 and Beloozerova et al. 2010), as suggested by the similarity of joint kinematics observed during the swing phase of forelimb motion in those studies and ours. The robustness of the revealed joint control strategy is also consistent with the similarity of the muscle activity patterns in the cat's forelimb between unperturbed locomotion and stepping over obstacles (Krouchev et al. 2006; Krouchev and Drew 2013). This robustness suggests that the use of the intersegmental dynamics of the limb through active rotation of the proximal joint may be a key component of most locomotion activities. The stability of this control structure simplifies neural control of locomotion because modifications in locomotion are achieved mainly through changes in control of a single joint. This control structure also provides flexibility of locomotion because changes only in control of the proximal joint modify motion of the entire limb. Changing control at a single joint at the very end of the swing phase enables swift locomotion adjustments in response to short-notice, unexpected perturbations that often emerge in real-world conditions.

Implications for neural control of movements. Our results support the interpretation that the brain exploits intersegmental dynamics of the lower extremities for movement production. Predominantly passive motion of the forelimb joints during the swing phase is consistent with a hypothesis that neural control minimizes muscle effort (Diedrichsen et al. 2010; Hatze and Buys 1977; Prilutsky and Zatsiorsky 2002; Ting and McKay 2007; Todorov 2004). However, our results question the importance of this optimization criterion during periods when active control is necessary. Indeed, the use of the shoulder for motion production requires overcoming inertia of the entire forelimb. Modification of step size by the distal rather than proximal joints would be advantageous in terms of reducing inertia of the controlled limb and hence, decreasing muscle effort, which was not observed in our study.

Alternatively, Dounskaia and Shimansky (2016) suggested that the advantage of the leading joint control structure is that it reduces neural effort for control of multi-joint movements by decreasing the amount of information that needs to be processed to provide joint coordination. This decrease is achieved by coordinating the trailing joints with respect to the leading joint motion largely passively. This interpretation is supported by the simplicity and flexibility of limb control provided by the use of the proximal joint as the leading joint during the swing phase of lower extremities discussed in the previous section. The control simplicity and flexibility may be prioritized because they likely reduce time for planning movement corrections and thus are advantageous when fast modifications are necessary in response to unexpected perturbations that threaten balance and locomotion. However, a compromise between the goals to minimize response time and muscle effort is also possible (Lu et al. 2012).

Dounskaia and Shimansky (2016) also showed that although the trailing joints move predominantly passively, the leading joint control structure allows production of accurate movements while maintaining low neural effort for limb control. This is achieved with low accuracy of the leading joint control and the use of the trailing joints to increase accuracy of the entire movement through small corrections. According to this interpretation, the shoulder was responsible for gross adjustments in the forelimb motion during the perturbed conditions. Although the passive torques played a crucial role in motion of the distal joints, MT was generated at these joints. It is possible that the purpose of this MT was to regulate passive motion of the trailing joints and provide small adjustments in the positioning of the paw on the cross-piece. Our previous study of neuronal responses conducted in the same cats (*cats 1* and *2*) during the same task is consistent with this interpretation. About 40% of motor cortical neurons exhibited a response during the known displacement condition (Stout et al. 2015a); however, during both unexpected displacement conditions, neurons with somatosensory receptive fields at the elbow or wrist became much more responsive, with nearly 70% of these subpopulations exhibiting a response, likely to provide corrections (Stout et al. 2015b).

Finally, Dounskaia and Shimansky (2016) predicted that neural resources used for movement control increase if the task requires a substantial modification of passive motion at the trailing joints through the use of active control. The ability of humans to predict and flexibly regulate and shape passive motion of trailing joints during arm movements has been demonstrated (Dounskaia et al. 1998, 2002, Galloway and Koshland 2002; Gribble and Ostry 1999). Cats did not make any substantial changes in control of the trailing joints (the elbow and wrist) in the present study despite the variety of the used conditions. Therefore, the ability to actively modify passive motion of trailing joints may be a feature of coordinated multi-joint movements that accounts for the more versatile motor repertoire in humans compared with animals.

APPENDIX

Contributions of the body translation and shoulder, elbow, and wrist rotations to end-point velocity were computed with an approach proposed by Sprigings et al. (1994) and Feltner and Nelson (1996) and used in our previous study (Kim et al. 2009). The end-point velocity ($\vec{V}_{ep}$) was calculated at each moment of time as

$$\begin{aligned}\vec{V}_{ep} &= \vec{V}_{bd} + \ \vec{\dot{\theta}}_{sh} \times \vec{l}_u + (\vec{\dot{\theta}}_{sh} + \vec{\dot{\theta}}_{el}) \times \vec{l}_f + (\vec{\dot{\theta}}_{sh} + \vec{\dot{\theta}}_{el} + \vec{\dot{\theta}}_{wr}) \times \vec{l}_p \\ &= \vec{V}_{bd} + \vec{\dot{\theta}}_{sh} \times \left(\vec{l}_u + \vec{l}_f + \vec{l}_p\right) + \vec{\dot{\theta}}_{el} \times \left(\vec{l}_f + \vec{l}_p\right) + \vec{\dot{\theta}}_{wr} \times \vec{l}_p, \quad (A1)\end{aligned}$$

where $\vec{V}_{bd}$ is the vector of the linear velocity of the body, $\vec{\dot{\theta}}$ is the vector of the angular velocity of each joint, and $\vec{l}$ is the vector pointing from the proximal to distal end of each forelimb segment. The subscripts *bd*, *sh*, *el*, and *wr* designate the body, shoulder, elbow, and wrist joints, respectively. The subscripts *u*, *f*, and *p* designate the forearm segments (the upper arm, forearm, and paw, respectively).

End-point velocity was attributed to four components of contribution: translational motion of the body and rotation of the shoulder, elbow, and wrist. The absolute magnitude of end-point velocity (speed of the toe) was calculated by the dot product of its unit vector

$$\left|\vec{V}_{ep}\right| = \vec{V}_{pw}\frac{\vec{V}_{ep}}{\left|\vec{V}_{ep}\right|} \qquad (A2)$$

Equations A1 and *A2* yield

$$\begin{aligned}\left|\vec{V}_{ep}\right| = \vec{V}_{bd}\frac{\vec{V}_{ep}}{\left|\vec{V}_{ep}\right|} + \left[\vec{\dot{\theta}}_{sh} \times \left(\vec{l}_u + \vec{l}_f + \vec{l}_p\right)\right]\frac{\vec{V}_{ep}}{\left|\vec{V}_{ep}\right|} + \vec{\dot{\theta}}_{el} \\ \times \left(\vec{l}_f + \vec{l}_p\right)\frac{\vec{V}_{ep}}{\left|\vec{V}_{ep}\right|} + \left[\vec{\dot{\theta}}_{wr} \times \vec{l}_p\right]\frac{\vec{V}_{ep}}{\left|\vec{V}_{ep}\right|},\end{aligned}$$

where the contribution of body translation is

$$\vec{V}_{bd}\frac{\vec{V}_{ep}}{\left|\vec{V}_{ep}\right|},$$

the contribution of shoulder rotation is

$$\left[\vec{\dot{\theta}}_{sh} \times \left(\vec{l}_u + \vec{l}_f + \vec{l}_p\right)\right] \frac{\vec{V}_{ep}}{\left|\vec{V}_{ep}\right|},$$

the contribution of elbow rotation is

$$\left[\vec{\dot{\theta}}_{el} \times \left(\vec{l}_f + \vec{l}_p\right)\right] \frac{\vec{V}_{ep}}{\left|\vec{V}_{ep}\right|},$$

and the contribution of the wrist rotation is

$$\left[\vec{\dot{\theta}}_{wr} \times \vec{l}_p\right] \frac{\vec{V}_{ep}}{\left|\vec{V}_{ep}\right|}.$$

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

H.N.Z. and I.N.B. performed experiments; H.N.Z., E.E.S., and N.D. analyzed data; H.N.Z., E.E.S., N.D., and I.N.B. interpreted results of experiments; H.N.Z., E.E.S., and I.N.B. prepared figures; H.N.Z., N.D., and I.N.B. edited and revised manuscript; H.N.Z., E.E.S., N.D., and I.N.B. approved final version of manuscript; E.E.S. and I.N.B. conceived and designed research; N.D. drafted manuscript.

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