*J Neurophysiol* 94: 2959–2969, 2005.
First published May 11, 2005; 10.1152/jn.00704.2004.



# Quantification of Motor Cortex Activity and Full-Body Biomechanics During Unconstrained Locomotion

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Submitted 9 July 2004; accepted in final form 6 May 2005

**Prilutsky, Boris I., Mikhail G. Sirota, Robert J. Gregor, and Irina N. Beloozerova.** Quantification of motor cortex activity and full-body biomechanics during unconstrained locomotion. *J Neurophysiol* 94: 2959–2969, 2005. First published May 11, 2005; 10.1152/jn.00704.2004. Recent progress in the understanding of motor cortex function has been achieved primarily by simultaneously recording motor cortex neuron activity and the movement kinematics of the corresponding limb. We have expanded this approach by combining high-quality cortical single-unit activity recordings with synchronized recordings of full-body kinematics and kinetics in the freely behaving cat. The method is illustrated by selected results obtained from two cats tested while walking on a flat surface. Using this method, the activity of 43 pyramidal tract neurons (PTNs) was recorded, averaged over 10 bins of a locomotion cycle, and compared with full-body mechanics by means of principal component and multivariate linear regression analyses. Patterns of 24 PTNs (56%) and 219 biomechanical variables (73%) were classified into just four groups of inter-correlated variables that accounted for 91% of the total variance, indicating that many of the recorded variables had similar patterns. The ensemble activity of different groups of two to eight PTNs accurately predicted the 10-bin patterns of all biomechanical variables (neural decoding) and vice versa; different small groups of mechanical variables accurately predicted the 10-bin pattern of each PTN (neural encoding). We conclude that comparison of motor cortex activity with full-body biomechanics may be a useful tool in further elucidating the function of the motor cortex.

## INTRODUCTION

Progress in understanding motor cortex function has been achieved largely by simultaneously recording the activity of motor cortex neurons and the mechanics of corresponding movements. Because of technical constraints, however, most studies have used motor tasks with one, two, or three degrees of freedom, such as manipulating objects with the hand (Evarts 1968), exertion of isometric forces (Ashe 1997), and reaching by the arm (Georgopoulos et al. 1982). These types of studies have revealed that the activity of the neuronal population of the motor cortex is related to different mechanical variables of motor tasks. For example, Evarts (1968) demonstrated in monkeys executing simple wrist movements that the activity of some neurons in the motor cortex was related to the activation of wrist flexor and extensor muscles. Motor cortex activity has also been found to be well correlated with other movement variables, e.g., the direction and velocity of movement (Georgopoulos et al. 1982; Moran and Schwartz 1999; respectively), the direction and magnitude of the static force exerted by the arm (Ashe 1997), the hand location in space (Sergio and Kalaska 1997), the arm orientation (Scott and Kalaska 1997), and the joint torque and power (Scott et al. 2001).

Mechanically constrained paradigms employed in the above-mentioned studies have allowed for the accurate and detailed determination of mechanical aspects of the task and their comparison with motor cortex activity. The motor cortex may also encode some parameters of multi-joint, full-body behavior (e.g., Donchin et al. 2002; Kalaska and Drew 1993). Simultaneous recording of motor cortex activity and body biomechanics in freely moving animals is required to test this suggestion, however.

Methods for recording the activity of the motor cortex in freely moving animals have been developed (Armstrong and Drew 1984; Beloozerova and Sirota 1986; Buzsaki et al. 1989; Girman 1973). Using these methods in cats revealed that the activity of most pyramidal tract neurons (PTNs) during locomotion on a flat surface is rhythmically modulated with respect to phases of the step cycle. A detailed movement analysis is more challenging in freely moving animals than during tasks with a limited number of degrees of freedom. For this reason, motor cortex activity during unconstrained movements typically has been analyzed in conjunction with muscle activation and simple kinematics of the contralateral limb (e.g., Drew 1988).

We believe that simultaneous recordings and analyses of motor cortex activity and full-body biomechanics during unconstrained animal behavior will provide a better understanding of motor cortex functions. PTNs, which have widespread connections onto the interneurons and motoneurons of a number of muscles of the contralateral limb (Georgopoulos and Grillner 1989; Lawrence et al. 1985; Leblond et al. 2001; Shinoda et al. 1986), are likely to control different aspects of movement through complex spinal networks. In addition, extensive branching of corticospinal axons in the brain stem and spinal cord (Armand 1982; Armand et al. 1985; Canedo 1997; Futami et al. 1979) suggests that PTN activity may affect not only the motor aspects of the contralateral limb but also those of the other three limbs. Examples of such effects might include full-body postural responses to voluntary gait modifications made by one limb during obstacle overstepping (Lavoie et al. 1995) and posture correction responses on a tilting surface (Beloozerova et al. 2005). Recently, encoding and decoding of global movement variables have been reported for neurons of the dorsal spinocerebellar tract (Bosco and Poppele

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elucidate the primary variables encoded in motor cortex activity. This might partly explain why this problem remains unresolved despite significant effort. In addition, the motor cortex contains groups of cells that appear to encode different aspects of motor behavior, including nonmotor aspects, in both extrinsic and different intrinsic (joint angle, muscle) coordinates (Alexander and Crutcher 1990; Carpenter et al. 1999; Kakei et al. 1999). Some of these cells might be among the 19 PTNs not classified into the four groups by the principal component analysis in this study. Still another problem is that the discharge of some PTNs appears to encode different parameters under different conditions (e.g., Beloozerova et al. 2005; Kakei et al. 2003; Sergio and Kalaska 2003; Thach 1978).

Despite their limitations, correlation and in particular multivariate regression analyses (Hamm et al. 2001; Holdefer and Miller 2002; Houk et al. 1987; Schwartz and Adams 1995; Stein et al. 2004) have been used extensively and have provided valuable information regarding representations of movement variables in motor cortex activity.

The developed method of simultaneously recording PTN activity and full-body mechanics provided new information on possible relationships between motor cortex activity and movement biomechanics. The fact that 73% of the full-body mechanical variables were highly correlated with one of the four eigenvectors, as revealed by the principal component analysis (Fig. 8), indicates that these patterns are redundant, i.e., many of the variables are closely correlated. As a consequence, a comparison of a limited number of mechanical variables with neural activity might yield misleading results. On the other hand, activation patterns of only 56% of sampled PTNs could be related to the four eigenvectors. The remaining 44% of neurons have patterns that differ from the majority of full-body mechanical variables and might encode information that is not directly related to motor patterns. These PTN activation patterns could also be related to muscles not sampled in this study.

Given the great number of mechanical variables obtained in this study, perhaps it is not surprising that it was possible to find subsets of variables that could accurately predict the firing rate of each sampled PTN. Accurate predictions of mechanical variables by the ensemble activity of a small number of PTNs could also be explained by the majority of these variables having relatively simple patterns (with 1–3 peaks per cycle). However, whether or not these predictions are real and not caused by chance will require further studies.

### *Limitations and advantages of the method*

The main limitations of the described experimental approach are the high complexity of the employed experimental procedures and the huge volume of information to be analyzed. The experimental procedures involve a combination of two innovative methods, analysis of full-body mechanics, and recording of PTN activity in unrestrained animals and thus require expertise in both areas of research. The motion analysis requires digitizing the coordinates of 28 markers on the animal body and is time consuming, but it can be substantially simplified by using motion analysis systems with automatic digitizing capabilities, which are commercially available. The results presented in this report show that despite the limitations, the new experimental approach is manageable and can yield unique and useful data on the functions of PTNs.

In particular, the developed method allowed us for the first time to compare the kinetics (ground reaction forces, joint forces, moments, power) of the contralateral limb with PTN activity during unconstrained cat locomotion, to obtain and compare PTN activity with the kinematics and kinetics of the other three limbs, and to obtain and compare PTN activity with movement characteristics of the general center of mass in the cat. These new developments have the potential to reveal new information about the functions of the motor cortex. We wish to stress, however, that any single method must be complemented with other techniques to obtain any definite information regarding physiological functions.

ACKNOWLEDGMENTS

We thank P. Wettenstein for exceptional engineering assistance. We are grateful to Drs. T. Hamm and Y. Shimansky for critical review of an earlier version of the manuscript.

GRANTS

The research reported in this paper was supported by the Center for Human Movement Studies of Georgia Institute of Technology to B. I. Prilutsky and by National Institute of Neurological Disorders and Stroke Grant R01 NS-39340 to I. N. Beloozerova.

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