The motor system plays the violin: a musical metaphor inferred from the oscillatory activity of the α-motoneuron pools during locomotion

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Abstract

Despite substantial advances in the field, particularly resulting from physiological studies in animals, the neural mechanisms underlying the generation of many motor behaviors in humans remain unclear. A recent study by Cappellini and colleague sheds more light on this topic. Like the string of a violin, the α-motoneuron pools in the spinal cord during locomotion show continuous and oscillatory patterns of activation. In this report, the implications and relevance of this finding are discussed in a general framework that includes neurophysiology, optimal control theory and robotics.

Main text

Complex behaviors involve the coordination of many muscles and hence motor neuron activity. Previous studies have provided evidence that the patterns of co-activation of multiple muscles can be broken down into more basic units, usually referred to as muscle synergies (Chiovetto et al. 2010; Danion and Latash, 2010; d'Avella et al. 2003). This work has motivated the so-called "piano-model" of movement generation: according to this model, synergies can be thought of as the keys of a piano, on which a musician has to act to play a song. A severe limitation in this metaphor is however that it provides limited insight on how the keys of the piano might be related to particular spinal structures.

A recent study by Cappellini and colleagues (2010) has provided some new remarkable findings, in the framework of locomotion, which might shed more light on this question. Their work however suggests a metaphor that relates more to the violin than the piano. The authors studied the relationship between the spinal motor output and the mechanics associated with the whole-body

center of mass (CoM) during walking and running. They recorded the electromyographic activity (EMG) of thirty bilateral leg muscles during different kinds of gait, and mapped such EMG patterns onto the spinal cord in approximate rostrocaudal locations of the motor neuron pools. In the human spinal cord, α-motoneurons (MNs) present a very specific topography: each muscle is innervated by several spinal segments, and each segment supplies several muscles. By using specific myotomal charts reporting the proportion of total muscle activation attributable to each spinal segment, authors could reconstruct the spatiotemporal patterns of the MNs and calculate the global center of activity (CoA) of the corresponding α-motoneurons in the lumbosacral enlargement.

The CoA computation method, which represents the most crucial point of the study, is based on strong assumptions. First, it assumes that rectified EMG provides an indirect measure of the net MNs firing of that muscle. Second, it assumes that the population of subjects has the same spinal topography. Moreover, the computation of the CoA location in the spinal cord depends directly on the EMG values and therefore different normalization procedures , which can generally be applied to muscle signals, may lead to different estimates of the CoA. In the analysis, authors recorded moreover the activity of only a subset of leg muscles, and this also might impair the accuracy of the estimation of the CoA position. Despite these multiple limitations however, authors were able to provide evidence against these possible pitfalls regarding the CoA computation. They showed that results basically did not change when different EMG normalization procedures were applied: this indicated that the functional topography of spinal cord activation was sufficiently robust. They assessed furthermore also parametric sensitivity of the method to the group of muscles considered and found that results did not change when one out of the thirty recorded muscles was excluded from the analysis.

Subsequently, the study tested whether the pattern of spinal cord activity could be related to high level features of motor coordination (the song played by the violin). The most natural place to start from was the body centre of mass (CoM), as its motion results from the displacement of all the segments of the body and hence all the lower-limb muscles. Cappellini and colleagues correlated directly the temporal evolution of CoA with the kinematic and kinetic energy of the CoM. Given the high level of non-linearity characterizing human body actuation, very complex behaviors of the CoA could be expected. For instance, one might expect five basic centers of oscillation of the CoA (matching the number of basis components found by Ivanenko et al. 2004 in the analysis of human subjects), or even more complex behaviors. The results, however, showed surprisingly that only two main temporal oscillations characterized the CoA displacement along the lumbosacral segment of the spinal cord.

These shifts were also found to mirror changes in the kinematic and potential energies of the CoM during both walking and running (see Cappellini et al. 2010, Fig. 5). The authors explained this correlation by the unique heel-to-toe rolling pattern that characterizes human gait during the stance phase. As a result of the shift of the body center of pressure under the foot indeed, the ground reaction force oscillates and its two components (vertical and horizontal) determine changes of both potential and kinetic energy associated with the CoM motion. Such a relationship between oscillation of the CoA and the biomechanics of human gait is also supported by two additional experimental conditions: walking on a slippery surface and walking backwards. In the first condition the shear force acting on the foot is strongly reduced, implying that CoA and kinetic energy do not oscillate. On the other hand, during the second condition the shear force is opposite to that generated during forward walking, producing a change of the muscle coordination. The results confirmed that, when walking on a slippery surface, there was no oscillation of the CoA or the kinetic energy.

Despite the relevance of the results presented by the authors, additional investigations and analysis might have been also carried out during the study. For instance, the set of experimental conditions could have been extended. It could indeed be very interesting to collect the EMG activity from the leg muscles of subjects walking on a treadmill and asked to keep a constant absolute position of the hips (and consequently of the CoM) along the direction of locomotion. In that case muscles should present very likely the same EMG pattern characterizing free walking, but the energetic features of the actual CoM should result deeply modified (kinetic energy approximately equal to zero). Moreover, the estimate the CoA location described above is only "apparent", as it is inferred indirectly from the pattern of muscle activity refracted through the projection pattern of the spinal α-MNs onto muscles. Experimental validation of the results could therefore be useful in the future, and obtained by means of more invasive recording techniques. Although these are difficult to apply to humans, recent technological developments (Berg et al. 2009) have made it possible to record MN activity directly from the spinal cord in awake and locomoting rats. In this framework, it would interestingly be possible to get some actual measures of the MN activity along the spinal cord with which to correlate the patterns of muscle activations. It might also be possible that such actual measures may reveal significant features of the pattern of MN activity that may not be captured with the indirect remapping of the EMG activity onto the spinal cord. More complex mathematical tools already used in literature in other animal studies (see for instance Hart and Giszter, 2010) might furthermore reveal more powerful for data analysis than a standard correlation approach based on the computation of the correlation coefficient.

There are multiple reasons that make the finding of the correlation between the movement of motor pool activity in the spinal cord and body mechanics during walking extremely interesting for the motor control community. In a previous study (Ivanenko at al. 2008), it was described how the

spatiotemporal patterns of ipsilateral α-motoneuron activity along the rostrocaudal axis relate to five basis muscle components which formed a basis for the accurate approximations of the muscle patterns recorded during different kinds of gait, including walking and running. This study showed that Gaussian-like components corresponded to temporal periods of activation of some MN pools in the lumbosacral enlargement. Moreover, such components could be associated with specific kinematic events, such as lift-off or touch-down. The work by Cappellini at al. (2010) complements such previous findings and provides evidence for a possible hierarchical organization of locomotion. Indeed, whereas the modular features characterizing EMG patterns during locomotion have already been described in detail, the mechanisms regulating the combination of such motor primitives have remained an open problem.

This study by Cappellini et al. (2010) suggests that the topological organization of NM activation in the spinal cord (summarized by the CoA, resembling the point of contact between the bow and the string of the violin) may represent the process according to which high-level control variables are translated into low-level control strategies at the level of the spinal motor neurons. The existence of central pattern generators (CPG) in the spinal cord capable of producing rhythmic activity in the absence of higher brain centers and sensory feedback is well documented in the literature (Grillner 1985). Cappellini and colleague offered a plausible explanation of the way CPG activity might be modulated to achieve the desired walking behavior.

The idea of a hierarchical control of gait generation is supported by other experimental results obtained by Lockhart and Ting (2007), which studied postural control in cats that reacted to a sudden support-surface motion. Authors demonstrated that neural command to multiple muscles were modulated by high-level, task related movement variables (CoM position, velocity and acceleration) through a low-dimensional feedback transformation, translating the requirements of CoM

stabilization into a modulation of muscle synergies. Importantly, Lockhart and Ting demonstrated that such a hierarchical controller is optimal, as it minimizes a specific cost function that minimizes the error between recorded and predicted EMGs and CoM kinematics. The results reported by Cappellini et al. (2010) make it difficult to infer directly whether the spatiotemporal pattern of activations of MNs in the spinal cord can be derived from an optimality criterion. Furthermore, locomotion involves completely different mechanisms from those required to fulfill postural tasks, since feed-forward control is mainly required in the first case, while a feedback control is required in the other.

Monaco et al. (2010) reported however (using the same mapping method exploited by Cappellini et al. 2010) that, although identical basic EMG primitives for walking were found in young and elderly people, the MN activity of the pools belonging to the lumbosacral enlargement differed between the two groups. Likely this could reflect age-related changes of both the central nervous system and the motor control strategy during locomotion. In most of the cases, elderly showed a marked decrease of the motor performances compared to younger people. Therefore, in light of these findings and in the framework of a hierarchical control of locomotion, the correlation between MN activity and the energetic features associated with the CoM in young and healthy subject might not be casual but oriented to fulfill some optimal energetic criteria. Additional investigations are however required to support this hypothesis.

Recently, attempts to drive locomotion of a bipedal humanoid robot by means of a series of coupled CPGs have also been made. Righetti and Ijspeert (2006) designed a control architecture in which each degree-of-freedom of a robot was controlled by a programmable CPG. By design, each one of them was coupled with other ones, in order to keep correct phase differences among the different degrees-of-freedom during locomotion. Righetti and Ijspeert demonstrated that such a control architecture could, after programmable CPGs had been trained by means of sample

trajectories of walk motion previously recorded, generate online joint trajectories assuring human-like walking features to the robot. Different trajectories could be generated by modulating the learned frequency and amplitude vectors associated with the CPGs. Such an approach to robot locomotion revealed therefore being highly biologically inspired and it could constitute a perfect platform to validate all the control hypotheses of human locomotion that have been discussed above.

In conclusion, the study by Cappellini and colleagues is interesting for many reasons. Most importantly, it provides neurophysiological results that motivate an extension of the classical metaphor that compares the generation of movements to the playing of a piano to that of a violin (Fig. 1). In both cases, the musician has to act on the discrete elements of his instrument (the keys of the piano or the strings of the violin) to play a song. When the musician plays the piano, however, the general temporal pattern according to which the different keys are pressed is difficult to understand. When the musician plays the violin, instead, the song is produced accordingly to oscillatory and continuous patterns of displacement of the bow over the strings. The movement of the bow is reminiscent of the oscillatory and "high-level features" that characterize the kinetic energy of the body's CoM, which (similar to the choice of stops on the violin) are translated into a muscle-specific low-level control strategy at spinal level to achieve the desired locomotor behavior.

References

Berg RW, Chen MT, Huang HC, Hsiao MC, Cheng H. A method for unit recording in the lumbar spinal cord during locomotion of the conscious adult rat. *J Neurosci Methods* 182:49-54, 2009.

Cappellini G, Ivanenko YP, Dominici N, Poppele RE, Lacquaniti F. Migration of motor pool activity in the spinal cord reflects body mechanics in human locomotion. *J Neurophysiol* 104:3064-73, 2010.

Chiovetto E, Berret B, Pozzo T. Tri-dimensional and triphasic muscle organization of whole-body pointing movements. *Neuroscience* 170:1223-38, 2010.

Danion F, Latash M. Motor control: theories, experiments and applications. New York: Oxford University Press, 2010.

d'Avella A, Saltiel P, Bizzi E. Combinations of muscle synergies in the construction of a natural motor behavior. *Nat Neurosci* 6:300 –308, 2003.

Grillner S. Neurobiological base of rhythmic motor acts in vertebrates. *Science* 228:143–149, 1985.

Hart CB, Giszter SF. A neural basis for motor primitives in the spinal cord. *J Neurosci* 30:1322–1336, 2010.

Ivanenko YP, Poppele RE, Lacquaniti F. Five basic muscle activation patterns account for muscle   activity during human locomotion. *J Physiol* 556: 267-282, 2004.

Ivanenko YP, Cappellini G, Poppele RE, Lacquaniti F. Spatiotemporal organization of alpha motoneuron activity in the human spinal cord during different gaits and gait transitions. *Eur J Neurosci* 27: 3351-3368, 2008.

Lockhart DB, Ting LH. Optimal sensorimotor transformations for balance. *Nat Neurosci* 10:1329 –1336, 2007.

Monaco V, Ghionzoli A, Micera S. Age-related modifications of muscle synergies and spinal cord activity during locomotion. *J Neurophysiol* 104:2092-102, 2010.

Righetti L, Ijspeert AJ. Programmable central pattern generators: an application to biped locomotion control. In Proceedings of the 2006 IEEE international conference on robotics and automation: 1585–1590, 2006.
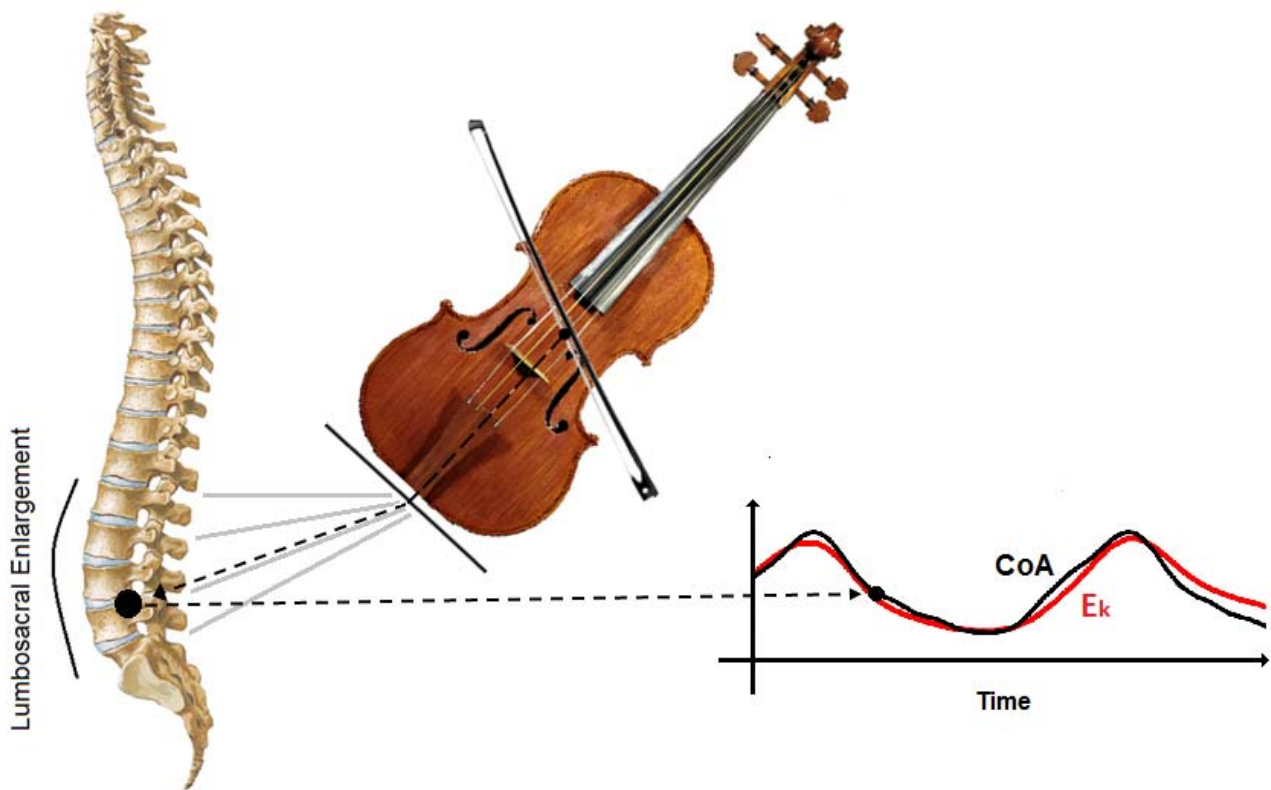
Figure 1: Schematic comparison between the spinal cord and the violin. During locomotion, the segments of the spinal cord can be thought as the strings of the violin and the CoA moving along the lumbosacral enlargement (black dot) can be compared to the point of contact between the bow and the strings. The musician has to draw continuously the bow across the strings of his instrument in order to create a meaningful song: this would correspond to a patterned oscillatory movement of the CoA position along the lumbosacral enlargement. This pattern can then be thought as driven by different high-level control variables (for instance, the temporal evolution of the kinetic energy E_k associated with the body CoM) and achieved by appropriate modulation of the activity of the CPGs in the spinal cord by the locomotor command systems of the brainstem. The temporal time series of CoA and E_k in the figure were taken from Cappellini et al. (2010) and refer to a real walking trial. The gray lines between the violin and the spinal cord indicate the correspondence between the strings of the violin and the spinal segments.