Studying the Nervous System Under Physiological Conditions. Focus on “Contribution of Force Feedback to Ankle Extensor Activity in Decerebrate Walking Cats”

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What is the contribution of proprioceptive force feedback in force generation during active movements? This question is of great interest for understanding how the CNS compensates for gravitational load (Duysens et al. 2000). As an animal walks, the weight on a given leg changes considerably during the stance phase. To compensate for this shift in weight, the motor command system needs to actively adapt the force exerted by the extensor muscles. Indeed, the interplay between centrally programmed activity and feedback activity has motivated research for almost a century (Pearson 1993). Such questions are difficult to address because they require the analysis of the functional role of neural components in a behaving animal. This is one of the merits of the paper by Donelan and Pearson, (this issue, p. 2093–2104). In mammals, the Golgi tendon organ constitutes a type of proprioceptor specialized in force detection. However, its quantitative contribution to load compensation during active movement has until now not been determined. Donelan and Pearson provide, for the first time, a quantitative estimation of the contribution of this type of force feedback to ankle extensor activity during walking.

This question is important because we know that most rhythmic movements of animals are produced by central pattern generators (CPGs) capable of producing patterned activity in the absence of any sensory feedback. CPGs have been described in virtually all vertebrate and invertebrate motor systems studied (Delcomyn 1980). In vitro, these CPGs produce programmed activity termed “fictive” walking, “fictive” swimming, etc., because no movements are produced during these centrally programmed activities (Viala et al. 1978). However, a striking feature of most of these fictive motor activities is their high degree of similarity with activities produced during true movements. What then is the role of sensory feedback in this kind of motor activity? Several roles have been acknowledged, such as precisely tuning the temporal output pattern (Prochazka et al. 1989), facilitating the transition from one phase to the next (Grillner and Rossignol 1978), and reinforcing the ongoing activity (Delcomyn 1980; Rossignol et al. 1988). Apart from this role in shaping the rhythmic motor command, in some extreme cases, proprioceptive feedback cues are so intimately linked to the CPG that proprioceptors can be considered as elements of the rhythmic generator; this was shown for the edge cells in the lamprey spinal cord (Grillner et al. 1991; Rossignol et al. 1988) and the wing stretch receptors of the locust flight system (Pearson 1985).

In this paper, Donelan and Pearson have studied load compensation in the walking system of the cat. Previous work has shown that, during the stance phase, the extensor activity was reinforced by increasing length or load of the muscle (Akazawa et al. 1982; Bennett et al. 1996). Two proprioceptive structures could be involved in this phenomenon: muscle spindle afferents (via Ia sensory fibers) and Golgi tendon organ (via Ib sensory fibers). Two sets of observations indicate that these sensory structures could be involved: 1) both group Ia and group Ib afferents are activated during the stance phase (Prochazka and Gorassini 1998; Prochazka et al. 1989), and 2) the electrical stimulation of group I afferents from ankle extensor muscles prolongs the stance phase and prevents transition to the swing phase (Whelan 1996; Whelan et al. 1995). However, in these experiments, no quantification of the participation of each of these proprioceptive afferents was done.

Using a decerebrate cat walking on a treadmill, the authors varied the length of the isolated medial gastrocnemius (MG) muscle (an extensor of the ankle) during sequences of rhythmic contractions associated with walking in the three other legs. They found that both muscle activity and force increased as the muscle was elongated. The key point of their demonstration consists of differentiating two regions in the EMG from the MG muscle during walking: an early region and a middle region. The increased muscle activity did not involve muscle spindles because, contrary to Golgi tendon organs, the activity of muscle spindles was relatively insensitive to changes in muscle length in the middle region of MG bursts. The authors also show that other proprioceptors, such as group II afferents, were not involved in this increased activity associated with increased force. These results indicate that the pathway of positive force feedback is mediated by the Golgi tendon organs and is isolated from other afferent pathways in their experimental paradigm. The authors propose a simple model of the neuromuscular system involved in load compensation that they use to estimate the gain of the force feedback loop. Using this model, they estimate that force feedback accounts for 20% of the total force at short muscle length (i.e., when walking on a horizontal surface), but may account for \( \leq 50\% \) of the total force at longer muscle length (i.e., when walking up slopes). The work of Donelan and Pearson highlights the role of force proprioception in the control of rhythmic movements. They show that it significantly contributes to the adaptation of the output of the nervous system to changing biomechanical constraints. This work is a stimulating example of the interest of studying the motor nervous system in its natural environment: the living animal.
REFERENCES


