Available online at www.sciencedirect.com

SciVerse ScienceDirect

ELSEVIER

Current Opinion in Neurobiology

Physiological and circuit mechanisms of postural control

Tatiana G Deliagina, Pavel V Zelenin and Grigori N Orlovsky

The postural system maintains a specific body orientation and equilibrium during standing and during locomotion in the presence of many destabilizing factors (external and internal). Numerous studies in humans have revealed essential features of the functional organization of this system. Recent studies on different animal models have significantly supplemented human studies. They have greatly expanded our knowledge of how the control system operates, how the postural functions are distributed within different parts of CNS, and how these parts interact with each other to produce postural corrections and adjustments. This review outlines recent advances in the studies of postural control in quadrupeds, with special attention given the neuronal postural mechanisms.

Address
Department of Neuroscience, Karolinska Institute, SE-17177 Stockholm, Sweden

Corresponding author: Deliagina, Tatiana G (Tatiana.Deliagina@ki.se)

Current Opinion in Neurobiology 2012, **22**:1–7

This review comes from a themed issue on
Microcircuits
Edited by Edward Callaway and Eve Marder

0959-4388/$ – see front matter

DOI 10.1016/j.conb.2012.03.002

Introduction

Animals and humans actively stabilize a definite body orientation in space due to activity of the postural system. In higher vertebrates, it is important for standing and walking, as well as for providing support of voluntary movements [1]. Control of posture is an evolutionarily old motor function. Detailed analysis of neuronal networks responsible for stabilization of body orientation in space has been performed in simpler animal models (lower vertebrates and invertebrates) [2,3]. These studies revealed remarkable similarities in the organization and operation of postural networks in these evolutionarily remote species. In contrast, our knowledge about postural networks in higher vertebrates is rather scarce. This review outlines recent advances in studying the mechanisms of postural control in quadrupeds during two motor behaviors — standing and walking. It is focused on the feedback mode of postural control (compensatory reactions to unexpected postural perturbations). For recent advances in the field of feed-forward postural control (postural adjustments accompanying voluntary movements) see [4–10].

Postural control during standing

In this section, we consider operation of the postural control system during standing in three postural tasks with different unexpected perturbations — lateral tilt of the support surface, translation of the support surface, and drop of the limb support.

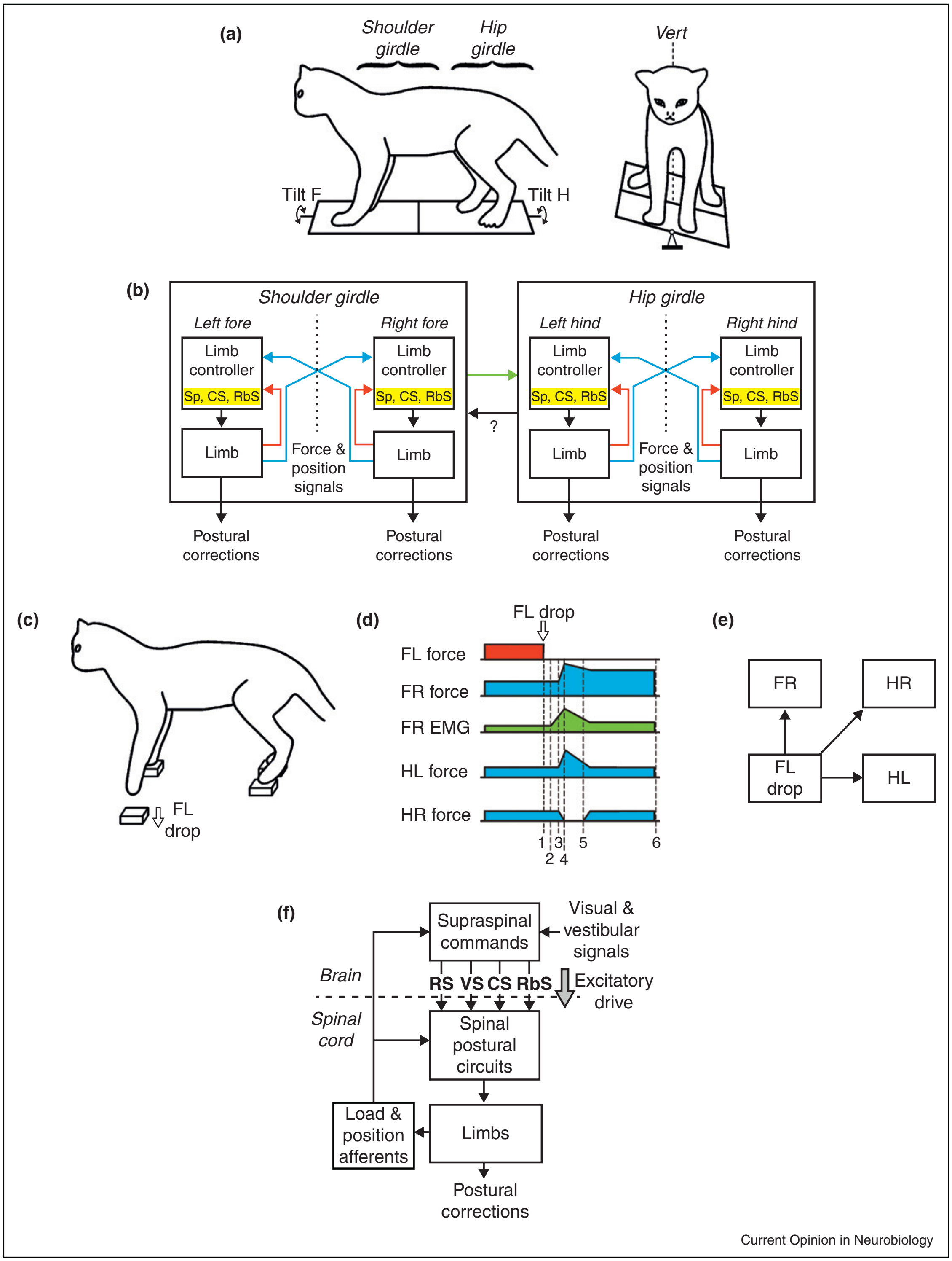
Compensatory postural reaction to lateral tilt of support surface

A lateral tilt of the support surface causes a lateral body sway and evokes a compensatory postural reaction — extension of the limbs on the side moving down and flexion of the limbs on the opposite side, which moves the dorso-ventral trunk axis toward the vertical (Figure 1a) [11,12,13•]. This postural reaction is not a gradual function of the tilt angle; the underlying mechanisms possess both threshold and plateau properties [12]. The somatosensory inputs from the limbs play a major role for elicitation of postural reactions to tilts [11,12] except for very fast tilts [14]. However, a tonic vestibular input is important for operation of postural mechanisms [15], and asymmetry in the right and left inputs (produced by galvanic stimulation of vestibular organs, that is, transcranial direct current stimulation that affects vestibular afferents) shifts a set-point in the postural reflex mechanisms [16], resulting in a change in the stabilized trunk orientation [12]. Similar mechanisms for changing the stabilized body orientation were found in simpler animals models [2,3]. It has been shown [12,13•] that the system generating postural corrections consists of two semiautonomous subsystems stabilizing the anterior and posterior parts of the trunk. Each subsystem contains two limb controllers generating corrective limb movement in response to sensory input from the same limb (see Figure 1 legend for details). Such a functional organization is similar to that of the locomotor system in quadrupeds [17].

It has been demonstrated that the basic mechanisms generating corrective postural reactions to tilts reside at the lower levels of CNS, with the brainstem and cerebellum playing a key role [18–20]. However, essential elements of these reactions — postural limb reflexes (PLRs) — can be evoked in acute spinal rabbits (transection of the spinal cord was done in the T12 segment) subjected to electrical stimulation of the spinal cord [19•], though the PLR magnitude was reduced. These findings suggest that the PLR-generating networks reside in the spinal cord and, in intact animals, are activated by tonic

Please cite this article in press as: Deliagina TG, et al.. Physiological and circuit mechanisms of postural control, Curr Opin Neurobiol (2012), doi:10.1016/j.conb.2012.03.002

Figure 1



Reactions of the postural system to different perturbations. **(a)** Postural task with lateral tilts of the support surface. The cat is keeping balance on two platforms (fore and hind) tilted together or independently. **(b)** Functional model of the postural system in the task with lateral tilts. Lateral stability of the anterior and posterior parts of the body (shoulder and hip girdles) is maintained by two relatively independent subsystems. Each subsystem contains two controllers (for the right and left limbs) generating a part of corrective limb movement in response to sensory input from the same limb (red lines); another part is produced in response to influences from the contralateral limb (blue lines). Coordination between these subsystems is primarily based on influences of the anterior subsystem on the posterior one (green lines). **(c)** Postural task with removal of the support surface under the left forelimb (FL). **(d)** Postural reaction (forces and EMGs in individual limbs) to drop of FL, and timing of the events: 1, drop of FL; 1–2, latency of FR EMG; 1–3,

Please cite this article in press as: Deliagina TG, et al.. Physiological and circuit mechanisms of postural control, Curr Opin Neurobiol (2012), doi:10.1016/j.conb.2012.03.002

excitatory drive from posture-related structures (such as ventral tegmental field and mesencephalic locomotor region [18,21]). Based on these results, a search for the factors enhancing PLRs in subjects with spinal cord injury (and, therefore, promoting restoration of their lateral stability) was initiated [20,22].

Recent studies provided essential information about activity of spinal postural networks [16,23]. Recordings from spinal interneurons during PLRs in decerebrate rabbits (the brain was removed rostral to precollicular-postmammilary level) revealed two populations of neurons with reciprocal responses to tilts. These responses were primarily determined by somatosensory input from the ipsilateral limb. In the framework of the functional model (Figure 1b) these neurons belong to the limb controllers. Temporal elimination of supraspinal influences by a cold block, which resulted in dramatic reduction in PLRs, caused diverse effects on individual neurons but, on average, their responses to tilts considerably decreased [23]. Thus, supraspinal influences make an essential contribution to the generation PLRs.

Of four major descending systems (Figure 1f), two systems (corticospinal, CS, and rubrospinal, RbS) were investigated in intact cats during postural reactions to tilts [24,25•]. The activity of 90% of CS neurons and 40% of RbS neurons was correlated with postural reactions, suggesting their contribution to these reactions. In the majority of neurons, modulation of their activity was primarily determined by the tilt-related somatosensory input from the projection (contralateral) limb [25•,26]. One can suggest that, in the framework of the functional model (Figure 1b), CS and RbS neurons belong to the limb controllers, and thus they are primarily involved in the intra-limb coordination and much less in the inter-limb coordination. Recordings from different types of cortical neurons during postural corrections [27•] have shown that responses of corticofugal neurons of layer 5 and local GABA-ergic interneurons are strongly correlated with postural corrections, whereas the activity of other neuronal types (e.g. projecting to the opposite hemisphere) was very weak, suggesting that cortical processing of the tilt-related information does not require interaction of the two hemispheres, in contrast to the task of postural control during reaching [28]. It was also shown that the GABA-ergic interneurons did not play any significant role in the modulation of CS neurons [29], raising a question about its origin.

Compensatory postural reaction to translation of support surface

In standing subjects, horizontal translation of the support surface causes a displacement of the limbs relative to the trunk. This distortion of posture evokes a corrective reaction that displaces the body and restores the normal trunk-limb configuration. A detailed analysis of this reaction was done in the cat [30,31•]. In response to translations in 16 different directions, each limb generated forces similar in direction but different in amplitude (''force constrain strategy'') [30]. Individual muscles responded in a wide range of perturbation angles [31•]. The observed muscle pattern can be described as a combination of four muscle synergies, which are active predominately during forward, backward, right, and left perturbations [32]. Essential features of this strategy persisted in decerebrate cats [33•,34], but responses were dramatically reduced in spinal cats [35,36], suggesting a crucial role of supraspinal phasic commands and tonic drive. Bilateral vestibular loss did not affect postural reactions to translation [37•]. By contrast, the loss of thick afferent fibers from limbs resulted in considerable increase of response latency [38], and loss of cutaneous afferents decreased the response magnitude [39]. It was reported [40,41] that input from Group I and II muscle spindle afferents is critically important for directionally appropriate muscle activation in response to horizontal translations of one limb. Thus, in this task, the functional organization of the system seems to be similar to that in the tilt task, in which a considerable part of the corrective movement of the limb is generated in response to sensory input from the same limb (Figure 1b).

Compensatory postural reactions to drop of support

In the standing cat, removal of the support surface under one of the limbs produced postural reactions, which resulted in transition from quadrupedal to tripedal standing [42–44] (Figure 1c,d). It was found that initial changes in EMG activity in three supporting limbs occurred at short latency (interval 1–2 in Figure 1d) and often preceded changes in the vertical force in these limbs. Since vestibular input does not contribute to initiation of postural reactions in this task [44••], these findings indicate that the initial postural changes in the supporting limbs (interval 2–3) are caused by sensory information from the dropping limb (Figure 1e). The subsequent EMG pattern, which underlies transition from diagonal to tripedal standing (interval 3–5), is most likely based on sensory information from the supporting limbs (as in the system responding to lateral tilts, Figure 1b). Recently, the

latency of FR force; 2–4, displacement of the center of mass over two diagonal supporting limbs; 4–5, transition from bipedal to tripedal support pattern; 5–6, maintenance of a stable posture and equilibrium over three supporting limbs. **(e)** Configuration of the system generating the early EMG responses to drop of FL (period 1–3). Later (period 3–5) the sensory inputs to supporting limbs are changed. **(f)** Main components of the postural system in quadrupeds. Two closed-loop mechanisms participate in the postural control. Spinal circuits generate postural limb reflexes, and their effects are added to the effects of supraspinal commands, which are generated on the basis of sensory information, and transmitted by the major descending tracts — reticulospinal (RS), vestibulospinal (VS), corticospinal (CS), and rubrospinal (RbS).

Please cite this article in press as: Deliagina TG, et al.. Physiological and circuit mechanisms of postural control, Curr Opin Neurobiol (2012), doi:10.1016/j.conb.2012.03.002

activity of reticulospinal (RS) neurons during postural reactions to drop of support was recorded in the cat [44••]. The majority of neurons responded to perturbation with a short latency and discharged before the initial change in EMG, suggesting that they participate in the initiation of corrective reactions. The striking result was that many individual RS neurons responded to drop of different limbs, thus contributing to generation of different specific postural reactions. One can suggest that these RS neurons generate a 'GO' command, and the motor response to this command depends on the current state of spinal networks affected by specific supraspinal and somatosensory inputs. Another possibility is that muscle groups activated by these RS neurons contribute to different postural reactions. Such mechanism was found in a lower vertebrate animal, the lamprey [45••].

Postural control during locomotion

In this section, we consider operation of the postural system during locomotion, in two different tasks — rapid reactions to lateral pushes and postural adaptations to the inclined support surface.

Compensatory reactions to lateral push

In cats walking on a treadmill, application of a lateral pulse of force (push) to the hip or shoulder girdle caused lateral sway of the corresponding part of the trunk, with a subsequent return to the initial position due to a change in the step pattern in one of the limbs of the corresponding girdle [46•]. A corrective step was performed by the limb that, at the moment of push, was at the end of stance phase or at the beginning of swing. In this step, a lateral component appeared in the swing trajectory due to the activity of muscles (abductors and adductors) moving the limb in the transverse plane. The step was directed either inwards or outwards, depending on the laterality of push. Because of the corrective step, the base of support appeared modified as compared to ordinary steps, and the limb position occurred more favorable for counteracting the body sway; as a result, the lateral stability was restored.

These postural corrections are generated by a mechanism in one girdle. The corrective step is well incorporated into the basic locomotor pattern: it only slightly affects the duration of step cycle and its structure. These results were basically similar to those obtained by translation of the support surface under the walking cats [47] and humans [48,49]. Cutaneous input is important for scaling the response but does not affect its latency and direction of step [50•], as in the task of surface translation during standing [39]. Since spinal animals are capable of sideward walking on the sideward moving treadmill [51], it seems likely that lateral corrective steps of a limb are generated by a spinal locomotor mechanism, and the step direction (inward/outward) is determined by sensory input from the opposite limb signaling its adduction/abduction caused by the postural perturbation.

Postural adaptation to inclined surface

To keep balance when walking on a surface inclined laterally, the cat modifies the limb configuration so that the functional length of the limbs increases on the side tilted down, and decreases on the opposite side. These changes in limb configuration are due to opposite changes of the EMG amplitude in the identical muscles of the right and left limbs, whereas the EMG timing remains basically unchanged [52•,53].

Participation of different descending systems in formation of the left/right asymmetry was assessed by recording vestibulospinal (VS), RS and CS neurons in the walking cat [52•,53]. Tilts of the treadmill evoked *positional responses* in CS, RS, and VS neurons, that is, changes in the amplitude of their modulation. These responses are most likely caused by somatosensory inputs from the limbs [52•,53]. Individual neurons in all three systems could be activated by ipsilateral or contralateral tilt. Tilt caused a change in the pattern of locomotor modulation in many RS neurons, whereas in CS and VS neurons it was barely affected. Thus, all three tested descending systems are involved in postural adaptations to specific features of the walkway. However, specific roles of these three descending systems for postural adaptations to the environment remain to be revealed. Comparing the positional responses to tilts in individual CS neurons during standing and walking suggests that both common and separate cortical mechanisms are used for postural adaptation to tilts in these two motor behaviors [53].

Conclusions and perspectives

1. Postural system in quadrupeds responds to numerous destabilizing factors by producing specific postural corrections. In the studied postural tasks, these corrections are caused mainly by somatosensory input from the limbs [11,12,13•,37•,44••,46•,52•,53], and the specific role of some afferent groups has been demonstrated [38–41,50•]. It has also been shown that the system generating postural corrections can dissociate into the semiautonomous subsystems stabilizing anterior and posterior parts of the trunk [12,13,46•]. The underlying neuronal mechanisms remain to be analyzed.
2. Postural corrections during locomotion are incorporated into the rhythmic pattern of limb movements [46•,47,52•,53]. In these modified steps, different characteristics can be changed: the step structure, step direction, EMG level, among others, but these changes do not disturb the locomotor rhythm. A problem of incorporation of a specific motor response into the ongoing locomotor pattern is common for different motor tasks, for example, voluntary gait modifications in the walking cat [4,54], and postural

Please cite this article in press as: Deliagina TG, et al.. Physiological and circuit mechanisms of postural control, Curr Opin Neurobiol (2012), doi:10.1016/j.conb.2012.03.002

reactions in the swimming lamprey [45••]. A detailed analysis of the integration of posture and locomotion is one of the major lines of future studies.

3. Recent studies have shown that the spinal cord can generate lateral steps [51] and PLRs [19•] in response to sensory inputs from the limbs signaling specific postural disturbance. One of the lines of future studies is the analysis of operation of spinal neuronal networks in different postural tasks, as well as a search for the factors enhancing their efficacy in spinal cord injured subjects. Another line is to understand how the capability of the spinal cord for sophisticated processing of somatosensory information [55,56] is used in different postural tasks.
4. Recent studies revealed two types of supraspinal influences: first, phasic postural commands [19,25•,44••] and second, tonic drive for activation of spinal postural networks [19•,20,23]. In a few examined postural tasks, phasic postural commands transmitted by CS, RbS, VS and RS tracts were analyzed, and different functions have been ascribed to CS and RbS neurons on one hand [25•,26], and to RS and VS neurons on the other [44••,52•]. The goal of future studies is to understand the neuronal mechanisms of formation of supraspinal postural commands, as well as their processing in the spinal networks, which results in the corrective motor response. Such mechanisms have been analyzed in considerable detail only in a lower vertebrate (lamprey) [3,45••].

Acknowledgements
This work was supported by grants from Swedish Research Council (no. 11554), the Christopher and Dana Reeve Foundation, NIH NS064964 to TGD, and by grant from Swedish Research Council (no. 21076) to PVZ.

References and recommended reading
Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Horak F, Macpherson J: **Postural orientation and equilibrium**. In *Handbook of Physiology. Exercise: Regulation and Integration of Multiple Systems.* Edited by Shepard J, Rowell L. New York: Oxford University Press; 1996:255-292.
2. Deliagina TG, Orlovsky GN, Zelenin PV, Beloozerova IN: **Neural bases of postural control**. *Physiology* 2006, **21**:216-225.
3. Deliagina TG, Beloozerova IN, Zelenin PV, Orlovsky GN: **Spinal and supraspinal postural networks**. *Brain Res Rev* 2008, **57**:212-221.
4. Prentice SD, Drew T: **Contributions of the reticulospinal system to the postural adjustments occurring during voluntary gait modifications**. *J Neurophysiol* 2001, **85**:679-698.
5. Schepens B, Drew T: **Strategies for the integration of posture and movement during reaching in the cat**. *J Neurophysiol* 2003, **90**:3066-3086.
6. Schepens B, Drew T: **Independent and convergent signals from the pontomedullary reticular formation contribute to the control of posture and movement during reaching in the cat**. *J Neurophysiol* 2004, **92**:2217-2238.
7. Schepens B, Drew T: **Descending signals from the pontomedullary reticular formation are bilateral, asymmetric, and gated during reaching movements in the cat**. *J Neurophysiol* 2006, **96**:2229-2252.
8. Scepens B, Stapley PJ, Dew T: **Neurons in the pontomedullary reticular formation signal posture and movement both as an integrated behavior and independently**. *J Neurophysiol* 2008, **100**:2235-2253.
9. Yakovenko S, Krouchev N, Drew T: **Sequential activation of motor cortical neurons contributes to intralimb coordination during reaching in the cat by modulating muscle synergies**. *J Neurophysiol* 2011, **105**:388-409.
10. Yakovenko S, Drew T: **A motor cortical contribution to the anticipatory postural adjustments that precede reaching in the cat**. *J Neurophysiol* 2009, **102**:853-874.
11. Deliagina TG, Beloozerova IN, Popova LB, Sirota MG, Swadlow H, Grant G, Orlovsky GN: **Role of different sensory inputs for maintenance of body posture in sitting rat and rabbit**. *Motor Control* 2000, **4**:439-452.
12. Beloozerova IN, Zelenin PV, Popova LB, Orlovsky GN, Grillner S, Deliagina TG: **Postural control in the rabbit maintaining balance on the tilting platform**. *J Neurophysiol* 2003, **90**:3783-3793.
13. • Deliagina TG, Sirota MG, Zelenin PV, Orlovsky GN, Beloozerova IN: **Interlimb postural coordination in the standing cat**. *J Physiol* 2006, **573**:211-224.
Activity of extensor muscles and contact forces under limbs were recorded in cats keeping equilibrium on the platform subjected to periodical lateral tilts under several conditions: (i) standing on four limbs (control); (ii) when one, two or three limbs were suspended and tilt-related somatosensory input from them was abolished; (iii) when the platforms under fore and hindlimbs were tilted in antiphase. Results of these tests allowed formulating the functional model of the system responsible for equilibrium control.
14. Macpherson JM, Everaert DG, Stapley PJ, Ting LH: **Bilateral vestibular loss in cats leads to active destabilization of balance during pitch and roll rotations of the support surface**. *J Neurophysiol* 2007, **97**:4357-4367.
15. Deliagina TG, Popova LB, Grant G: **The role of tonic vestibular input for postural control in rats**. *Arch Ital Biol* 1997, **135**:239-261.
16. Hsu L-J, Zelenin PV, Orlovsky GN, Deliagina TG: **Effect of galvanic stimulation on postural limb reflexes and neurons of spinal postural network**. *Soc Neurosci Abstr* 2011.
17. Orlovsky GN, Deliagina TG, Grillner S: *Neuronal Control of Locomotion. From Mollusc to Man*. Oxford: Oxford University Press; 1999.
18. Musienko PE, Zelenin PV, Lyalka VF, Orlovsky GN, Deliagina TG: **Postural performance in decerebrated rabbit**. *Behav Brain Res* 2008, **190**:124-134.
19. • Musienko PE, Zelenin PV, Orlovsky GN, Deliagina TG: **Facilitation of postural limb reflexes with epidural stimulation in spinal rabbits**. *J Neurophysiol* 2010, **103**:1080-1092.
In this study, the existence of spinal postural networks (responsible for postural limb reflexes, PLRs) was demonstrated. The PLRs were initially evoked in the decerebrated rabbit. These PLRs disappeared after acute spinalization at T12. However, after epidural electrical stimulation at L7, the PLRs reappeared and persisted for up to several minutes.
20. Lyalka VF, Hsu L-J, Karayannidou A, Zelenin PV, Orlovsky GN, Deliagina TG: **Facilitation of postural limb reflexes in spinal rabbits by serotonergic agonist administration, epidural electrocal stimulation, and postural training**. *J Neurophysiol* 2011, **106**:1341-1354.
21. Mori S: **Integration of posture and locomotion in acute decerebrate cats and in awake, freely moving cats**. *Prog Neurobiol* 1987, **28**:161-196.
22. Lyalka VF, Musienko PE, Orlovsky GN, Grillner S, Deliagina TG: **Effect of intrathecal administration of serotoninergic and noradrenergic grugs on postural performance in rabbits with spinal cord lesions**. *J Neurophysiol* 2008, **100**:723-732.

Please cite this article in press as: Deliagina TG, et al.. Physiological and circuit mechanisms of postural control, Curr Opin Neurobiol (2012), doi:10.1016/j.conb.2012.03.002

23. Deliagina TG, Zelenin PV, Karayannidou A, Orlovsky GN: **Effect of reversible spinalization on spinal neurons mediating postural limb reflexes**. *Soc Neurosci Abstr* 2009.

24. Beloozerova IN, Sirota MG, Orlovsky GN, Deliagina TG: **Activity of pyramidal tract neurons in the cat during postural corrections**. *J Neurophys* 2005, **93**:1831-1844.

25. • Zelenin PV, Beloozerova IN, Sirota MG, Orlovsky GN, Deliagina TG: **Activity of red nucleus neurons in the cat during postural corrections**. *J Neurosci* 2010, **30**:14533-14542.
In this study, individual rubrospinal (RbS) neurons were recorded in the cat standing on the tilting platform with different combinations of limbs (these postural tasks were described in [13•]). In all tasks in which the contralateral (projection) limb was suspended, and thus the tilt-related somasosensory input from this limb was absent, the tilt-related modulation in the majority of neurons considerably decreased. Similar results were obtained for corticospinal (CS) neurons [26]. These findings suggest that both RbS and CS systems are primarily involved in the intra-limb postural coordination, that is, in the feedback control of the corresponding limb and, to a lesser extent, in the inter-limb coordination.

26. Karayannidou A, Deliagina TG, Tamarova ZA, Sirota MG, Zelenin PV, Orlovsky GN, Beloozerova IN: **Influences of sensory input from the limbs on feline corticospinal neurons during postural responses**. *J Physiol* 2008, **586**:247-263.

27. • Beloozerova IN, Sirota MG, Swadlow HA, Orlovsky GN, Popova LB, Deliagina TG: **Activity of different classes of neurons of the motor cortex during postural corrections**. *J Neurosci* 2003, **23**:7844-7853.
This study was a first direct demonstration of involvement of motor cortex in feedback postural control. Five classes of cortical neurons [descending corticofugal neurons of layer V (CF5) and of layer VI (CF6); cortico-cortical neurons with ipsilateral projection (CCIs), and those with contralateral projections (CCCs); suspected inhibitory interneurons (SINs)] were recorded in rabbit during postural corrections caused by periodical lateral tilts of the supporting platform. Only CF5s and SINs were considerably active during the task and their activity was correlated with postural corrections.

28. Putrino D, Mastaglia FL, Ghosh S: **Neural integration of reaching and posture: interhemispheric spike correlations in cat motor cortex**. *Exp Brain Res* 2010, **202**:765-777.

29. Tamarova ZA, Sirota MG, Orlovsky GN, Deliagina TG, Beloozerova IN: **Role of $GABA_A$ inhibition in modulation of activity of pyramidal tract neurons during postural corrections**. *Eur J Neurosci* 2007, **25**:1484-1491.

30. Macpherson JM: **Strategies that simplify the control of quadruped stance. I. Forces at the ground**. *J Neurophysiol* 1988, **60**:204-217.

31. • Macpherson JM: **Strategies that simplify the control of quadruped stance. II. Electromyographic activity**. *J Neurophysiol* 1988, **60**:218-231.
This paper together with [30] was the first study in which postural reactions to horizontal translation of the support surface under standing cats were characterized. The 'force constraint' strategy was observed: the direction of force generated by each of the limbs was independent from the direction of perturbation. This same direction of the force was produced by different patterns of muscle activity that depended on the direction of translation.

32. Ting LH, Macpherson JM: **A limited set of muscle synergies for force control during a postural task**. *J Neurophysiol* 2005, **93**:609-613.

33. • Honeycutt CF, Gottschall JS, Nichols TR: **Electromyographic responses from the hindlimb muscles of the decerebrate cat to horizontal support surface perturbations**. *J Neurophysiol* 2009, **101**:2751-2761.
The decerebrate cat standing on a horizontal platform was subjected to the horizontal translation. The observed postural responses were similar to those in the intact cats, both in terms of the motor pattern (review [31•]) and the force-constraint strategy (review [30]). These results indicate a crucial role of the brainstem and spinal mechanisms in the control of stability in this task, and insignificant contribution of the cerebral cortex.

34. Honeycutt CF, Nichols TR: **The decerebrate cat generates the essential features of the force constraint strategy**. *J Neurophysiol* 2010, **103**:3266-3273.

35. Fung J, Macpherson JM: **Attributes of quiet stance in chronic spinal cat**. *J Neurophysiol* 1999, **82**:3056-3065.

36. Macpherson JM, Fung J: **Weight support and balance during perturbed stance in the chronic spinal cat**. *J Neurophysiol* 1999, **82**:3066-3081.

37. • Inglis JT, Macpherson JM: **Bilateral labyrinthectomy in the cat: effects on the postural response to translation**. *J Neurophysiol* 1995, **73**:1181-1191.
The cats after bilateral labyrinthectomy were able to stand and maintain balance during lateral translation of the support surface. The pattern of postural responses was similar to that observed in intact animals.

38. Stapley PJ, Ting LH, Hulliger M, Macpherson JM: **Automatic postural responses are delayed by pyridoxine-induced somatosensory loss**. *J Neurosci* 2002, **22**:5803-5807.

39. Honeycutt CF, Nichols TR: **Disruption of cutaneous feedback alters magnitude but not direction of muscle responses to postural perturbations in the decerebrate cat**. *Exp Brain Res* 2010, **203**:765-771.

40. Honeycutt CF, Stahl VA, Nichols TR: **Autogenic spindle pathways mediate the postural response during horizontal support surface perturbations**. *Soc Neurosci Abstr* 2007.

41. Honeycutt CF, Nardelli P, Cope TC, Nichols TR: **Loss of proprioceptive feedback from muscle disrupts the excitatory postural response to support surface perturbations**. *Soc Neurosci Abstr* 2008.

42. Dufossé M, Macpherson J, Massion J, Sybirska E: **The postural reaction to the drop of a hindlimb support in the standing cat remains following sensorimotor cortical ablation**. *Neurosci Lett* 1985, **55**:297-303.

43. Rushmer DS, Macphersom JM, Dunbar DC, Russell CJ, Windus SL: **Automatic postural response in the cat: responses of proximal and distal hindlimb muscles to drop of support from a single hind- or forelimb**. *Exp Brain Res* 1987, **65**:527-537.

44. •• Stapley P, Drew T: **The pontomedullary reticular formation contributes to the compensatory postural responses observed following removal of the support surface in the standing cat**. *J Neurophysiol* 2009, **101**:1334-1350.
This was the first study analyzing activity of individual reticulospinal (RS) neurons in the standing cat during a compensatory postural reaction caused by drop of the support under one of the limbs. The activity was correlated with different phases of the postural reaction. The majority of neurons responded to perturbations of more than one limb, suggesting that each of these neurons contributed to generation of different specific postural reactions. The data support the previously formulated hypothesis that motor effects of RS neurons depend on the state of the spinal network, which can also be affected by RS system [4,6–8]. It was suggested that sensory input from the dropping limb not only evokes RS commands but also changes the excitability of spinal targets of RS neurons.

45. •• Zelenin PV, Orlovsky GN, Deliagina TG: **Sensory-motor transformation by individual command neurons**. *J Neurosci* 2007, **27**:1024-1032.
This study first demonstrated the role of individual RS neurons in the sensory-motor transformation underlying postural corrections in a lower vertebrate (lamprey). It was shown that individual RS neurons transform sensory information about body orientation into the command that activates a specific combination of motoneuronal pools responsible for a specific postural correction. The closed-loop mechanisms formed by individual neurons operate in parallel to generate the resulting motor response.

46. • Karayannidou A, Zelenin PV, Orlovsky GN, Sirota MG, Beloozerova IN, Deliagina TG: **Maintenance of lateral stability during standing and walking in the cat**. *J Neurophysiol* 2009, **101**:8-19.
In this study, postural reactions in the cat to the same destabilizing stimulus (lateral push in the hip region), applied during standing and during walking, were compared. It was shown that principal mechanisms for balance control in these two forms of behavior are different. They perform a re-distribution of muscle activity between symmetrical limbs while standing, and a reconfiguration of the base of support (due to a lateral step) in walking. Adductor and abductor limb muscles are strongly involved in the generation of postural corrections in both behaviors.

Please cite this article in press as: Deliagina TG, et al.. Physiological and circuit mechanisms of postural control, Curr Opin Neurobiol (2012), doi:10.1016/j.conb.2012.03.002

47. Misiaszek JE: **Control of frontal plane motion of the hindlimbs in the unrestrained walking cat**. *J Neurophysiol* 2006, **96**:1816-1828.

48. Oddsson LI, Wall C, McPartland MD, Krebs DE, Tucker CA: **Recovery from perturbations during paced walking**. *Gait Posture* 2004, **19**:24-34.

49. Hof AL, Vermerris SM, Gjaltema WA: **Balance responses to lateral perturbations in human treadmill walking**. *J Exp Biol* 2010, **213**:2655-2664.

50. • Bolton DAE, Misiaszek JE: **Contribution of hindpaw cutaneous inputs to the control of lateral stability during walking in the cat**. *J Neurophysiol* 2009, **102**:1711-1724.

Ting and Macpherson [57] proposed that cutaneous signal from paw pads is ideal for triggering the rapid, direction-specific postural reaction to translation of the support surface. In this study, a contribution of cutaneous feedback from paws to generation of the response to lateral translation of the supporting surface was examined in the walking cat. It was shown that cutaneous inputs are important for scaling the response but not for its initiation.

51. Courtine G, Gerasimenko Y, van den Brand R, Yew A, Musienko P, Zhong H, Song B, Ao Y, Ichiyama RM, Lavrov I *et al.*: **Transformation of nonfunctional spinal circuits into functional states after the loss of brain input**. *Nat Neurosci* 2009, **12**:1333-1342.

52. • Matsuyama K, Drew T: **Vestibulospinal and reticulospinal neuronal activity during locomotion in the intact cat. II. Walking on an inclined plane**. *J Neurophysiol* 2000, **84**:2257-2276.

In this study, individual reticulospinal (RS) and vestibulospinal (VS) neurons were recorded in the cat walking on an inclined plane (up/down-hill or left/right tilt), which required specific modifications of the locomotor pattern. In both RS and VS neurons, surface inclination caused a change in the amplitude of descending signal. In VS neurons, it did not evoke any major change in the temporal pattern of step-related modulation. By contrast, in RS neurons, the pattern of modulations changed depending on the surface inclination. The authors discuss the possible functional roles of the two systems for postural adaptation to the inclined surface during locomotion.

53. Karayannidou A, Beloozerova IN, Zelenin PV, Stout EE, Sirota MG, Orlovsky GN, Deliagina TG: **Activity of pyramidal tract neurons in the cat during standing and walking on an inclined plane**. *J Physiol* 2009, **587**:3795-3811.

54. Drew T, Jiang W, Widajewicz W: **Contributions of the motor cortex to the control of the hindlimbs during locomotion in the cat**. *Brain Res Rev* 2002, **40**:178-191.

55. Poppele R, Bosco G: **Sophisticated spinal contributions to motor control**. *Trends Neurosci* 2003, **26**:269-276.

56. Bosco G, Eian J, Poppele RE: **Phase-specific sensory representations in spinocerebellar activity during stepping: evidence for a hybrid kinematic/kinetic framework**. *Exp Brain Res* 2006, **175**:83-96.

57. Ting LH, Macpherson JM: **Ratio of shear to load ground-reaction force may underlie the directional tuning of the automatic postural response to rotation and translation**. *J Neurophysiol* 2004, **92**:808-823.

Please cite this article in press as: Deliagina TG, et al.. Physiological and circuit mechanisms of postural control, Curr Opin Neurobiol (2012), doi:10.1016/j.conb.2012.03.002