DOI 10.1007/s11055-015-0062-3
Neuroscience and Behavioral Physiology, Vol. 45, No. 2, February, 2015

Regulation of Posture and Locomotion in Decerebrate and Spinal Animals

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Translated from Rossiiskii Fiziologicheskii Zhurnal imeni I. M. Sechenova, Vol. 99, No. 3, pp. 392–405, March, 2013. Original article submitted November 27, 2012.

The experiments reported here showed that decerebrate cats can actively maintain posture during standing and walking. On standing, postural corrections consisted of redistribution of extensor muscle activity in response to perturbations. Correcting reactions during walking included changes in the durations of the swing and transfer phases of the locomotor cycle, modulation of supporting force reactions, and modification of flexor and extensor function. Detailed analysis of correlations between muscle activity, supporting force reactions, and the kinematics of truncal and hindlimb movements showed that the motor system of the decerebrate animal can use a combination of feedback and feedforward to regulate dynamic balance during locomotion. Furthermore, balance was rapidly restored after impairment due to stumbling or perturbing influences. The intraspinal neural networks and somatosensory afferent input from the limbs can effectively regulate balance during walking and standing, without involvement of the vestibular and visual systems. After interruption of the connection with the motor centers of the stem and forebrain in decerebrate and spinal animals, these networks were in a suppressed state but could be activated by epidural and sensory stimulation substituting for tonic supraspinal drive.

Keywords: regulation of body posture, locomotion, decerebration, spinalization, brainstem motor centers, spinal motor system, electrical stimulation.

During standing and walking, animals and humans maintain the optimum body posture for balance. The automatic posture-regulating system is based on innate reflex mechanisms. The neural networks of the spinal cord and the motor centers of the brainstem are involved in posture control, though their significance remains poorly studied.

The posture regulation system works on the basis of the "closed loop" mechanism [10]. The "short loop" is located in the spinal cord: in response to a sensory input from mechanoreceptors in the limbs, it compensates for deviations in the main body posture by generating correcting movement responses (postural corrections). These responses can be regarded as signs of overlapping and non-overlapping spinal postural reflexes [26, 27]. The "long loop" includes the ascending and descending spinal pathways, the brainstem, and the cortex of the cerebral hemispheres [6, 7, 30, 31]. In addition to the mechanoreceptor signals, this mechanism receives vestibular and visual information and sends phasic correcting commands to the spinal cord via various descending pathways: the corticospinal, rubrospinal, reticu-

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lospinal, and vestibulospinal. These supraspinal commands evoke postural corrections, thus supplementing the spinal postural reflexes [19].

The relative involvement of the spinal and supraspinal mechanisms in stabilizing posture is unclear. Apart from phasic commands, the descending pathways also transmit tonic influences to the spinal cord, probably via the reticulospinal pathways, which activate spinal reflex networks [15, 30]. Identification of the role of the spinal-cerebral component of postural control and studies of the systems responsible for activating the spinal postural reflexes have high applied importance for developing methods for motor rehabilitation in paralyses due to spinal cord disease and trauma, which are often accompanied by serious postural abnormalities.

Recent years have seen successful attempts to produce artificial activation of spinal networks responsible for inducing locomotion and functional limb movements. Acute experiments on spinal frogs and rats have shown that many hindlimb motor patterns can be induced by electrical stimulation of particular areas of the gray matter of the spinal cord [14, 40]. Experimental data have been obtained showing that the spinal motor system consists of a multitude of functional "modules" (motor primitives), which combine to generate movements with different degrees of complexity [9, 41]. Chronic experiments on intact cats developed a method for microstimulating the lumbar bulge [36]. Stimulation of defined areas of the ventral quadrant of the spinal cord induced purposive contractions of particular muscles or muscle groups. This stimulation in spinal animals initiated more generalized responses, some cases showing gait with partial supporting of body weight [16]. Experiments using epidural electrical stimulation showed the effectiveness of this method for initiating locomotor activity in decerebrate and spinal animals [1, 3, 20].

The present studies on acute decerebrate and spinal cat models addressed: 1) the role of the brainstem motor centers and somatosensory systems in the integrative control of posture and locomotion; 2) postural reflexes in conditions of impaired supraspinal influences; and 3) the possibility of artificial activation of the spinal reflex postural control mechanisms using electrical stimulation of the spinal cord.

Methods

Experiments were performed on 10 decerebrate cats. All experiments were performed in compliance with "Regulations for Studies Using Experimental Animals" (USSR Ministry of Health Decree No. 755 of August 12, 1977) and the Law *On the Protection of Animals from Inhumane Treatment*, Chapter IV, article 10, 4679/11 GK of December 1, 1999.

Animals were subjected to general anesthesia and the trachea was intubated, the carotid arteries were ligated, and the animal was fixed in a stereotaxic apparatus; the skull was trepanned and decerebration was performed. Electromyogram (EMG) electrodes were then implanted, laminectomy was performed at the L2–L7 levels, an epidural electrode was placed, and kinematic markers were positioned in the projections of the hindlimb joints [1, 3, 13]. Functional state was monitored in terms of arterial pressure using an electromanometer connected to a cannula in the animal's carotid artery, as well as the ECG and rectal temperature.

The animals' head and anterior part of the trunk (T5–T7) were firmly fixed in the stereotaxic apparatus, leaving the posterior part of the body and hindlimbs free on the bench surface. Postural function was evaluated using the overall postural configuration of the body, the ability to perform righting adjustment reflexes, limb muscle tone, and the correctness and amplitudes of postural reactions for maintenance of balance on standing and walking. After experiments using the decerebrate model, complete transection of the spinal cord was performed at the lower thoracic level (T7–T9), and this was followed by analysis of the postural and locomotor capacities in acute spinal preparations [4].

Epidural stimulation with parameters optimum [3] for inducing stepping (stimulation frequency 5 Hz, stimulus duration 0.5 msec, current 100–300 μA) was performed with a wire electrode sutured to the dura mater at the level of spinal segment L5. The indifferent electrode was implanted in the paravertebral muscles. Stimulation was with an A-M Systems model 2100 stimulator. Bilateral recordings of electromyographic muscle activity in vastus lateralis (an extensor of the knee joint), tibialis anterior (a flexor of the ankle joint), and gastrocnemius (an extensor of the ankle joint) were made in a bipolar regime using stainless steel wire electrodes (AS632; Cooner Wire, Chatsworth, CA) implanted in the muscles of interest [13]. EMG signals were amplified using a differential amplifier (A-M Systems Model 1700) in the range 30 Hz to 10 kHz and digitized at 4 kHz with a National Instruments analog-to-digital converter, followed by analysis in LabView. Video recordings of the animals' movements were made simultaneously. The parameters of movement kinetics were analyzed in terms of changes in the positions of light-reflecting markers positioned on the skin in the projection of the pelvic, knee, and ankle joints and on the fifth toe. Tensometric probes were used to record the forces imposed on the support via the limbs. A mechanical sensor was used to record deviations of the lumbar segment in the lateral and vertical directions.

Quantitative characteristics (mean ± standard error) were calculated using standard statistics programs. Pearson correlation coefficients were used to identify relationships between pairs of variables. Statistically significant differences were identified using Student's t test at $p < 0.05$.

Results

Experiments with different levels of decerebration showed that the transection line was significantly reflected in movement capacities. Subthalamic animals with transection at the rostral superior colliculi and mammillary bodies were generally able to stand, walk, and support body weight independently. The overall configuration of body posture and the distribution of limb muscle tone were close to nor-

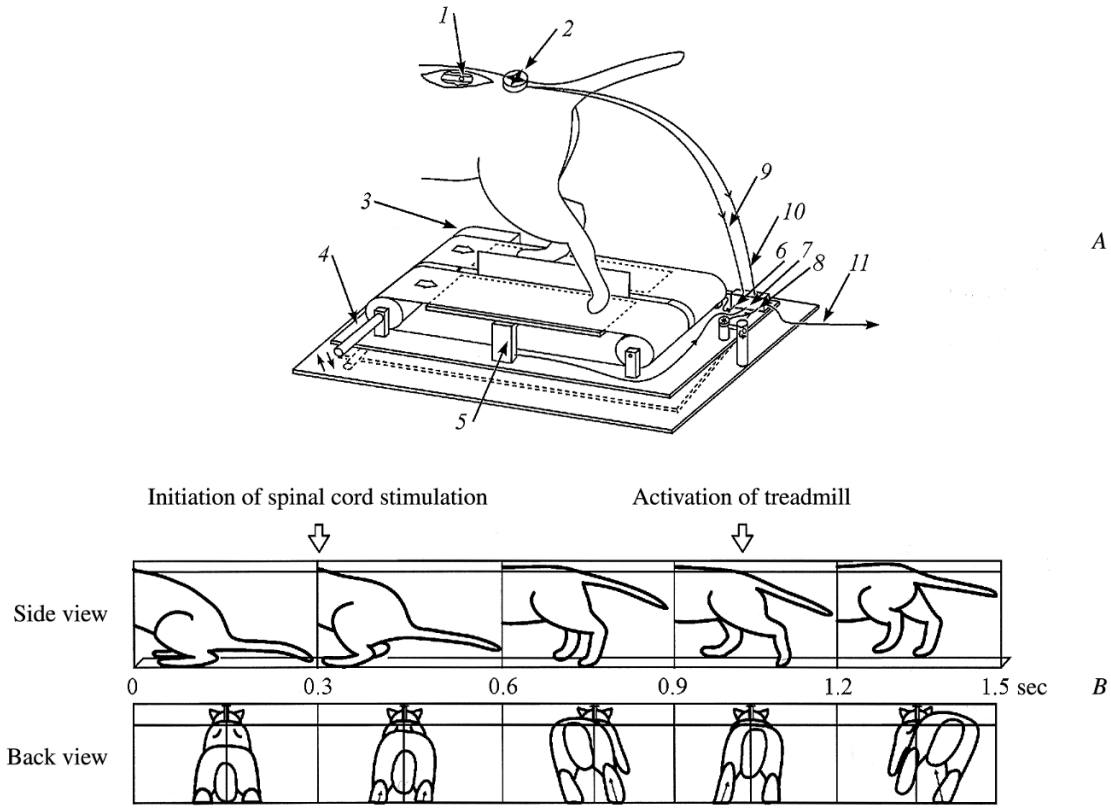

Fig. 1. Experimental apparatus and model of decerebration in cats for investigation of balance during walking. *A*) Experimental apparatus for studying maintenance of balance in a decerebrated cat: *1*) epidural electrode; *2*) probe for detection of deviation of the animal; *3*) impeller; *4*) treadmill tilt lever; *5*) sensory platform force probe; *6*) force signals recorded from the right side; *7)* force signals recorded from the left side; *8*) platform tilt angle; *9*) up-down cat deviation signal; *10*) lateral cat deviation signal; *11*) cable conducting all signals to the analog-to-digital converter. *B*) Standing and walking of a decerebrate cat with maintenance of body weight and balance; left and back views.

mal. The occurrence of spontaneous locomotion, interfering with postural tests, was characteristic. Animals with caudal transections passing through the pons were characterized by nonuniform distribution of muscle tone and decerebration rigidity. Further study of postural control was performed using precollicular-postmammillary decerebration (mesencephalic preparation, Shik technique [5]). In this situation, a normal distribution of muscle tone was seen, along with the absence of spontaneous locomotion. Initially decreased postural capacity could be activated by stimulation of the spinal cord. Stimulation at a frequency of 0.5–1 Hz and low amplitude (50–100 μA) increased muscle tone and postural responses while the animal was standing. Stimulation at greater frequency (3–5 Hz) and amplitude initiated locomotor activity. The integrative control of posture and locomotion in this preparation was studied using an apparatus developed for induction and recording of postural responses (Fig. 1, *A*). The apparatus consisted of an electromechanical stand treadmill and a set of probes for monitoring the body weight support function. The treadmill was positioned along an axis around which it could be tilted in the frontal plane. Sensory platforms located beneath each of the two treadmill bands measured the force with which the study object acted on the band during walking or standing. A series of mechanical sensors was used to record displacement of the animal's trunk and limbs in space.

Mesencephalic cats were unable to walk or stand spontaneously, and sat or lay passively on the immobile treadmill band before stimulation. The fact that the level of decerebration caudal to the optic tract switched off the visual input and rigid fixation of the head and anterior part of the body eliminated vestibular and minimized proprioceptive influences from the neck area made it possible to study the specific role of somatosensory signals from the limbs and trunk in the control of balance. Tonic electrical stimulation of the spinal cord at a frequency of 5 Hz and an amplitude of 100–300 μA evoked standing of the animal, developing on activation of the treadmill into true walking with complete body weight support (Fig. 1, *B*). On walking, cats deviated laterally but did not fall, maintaining balance. Motor responses on the right and left were compensated for by temporary shifting of the center of gravity from the balance point.

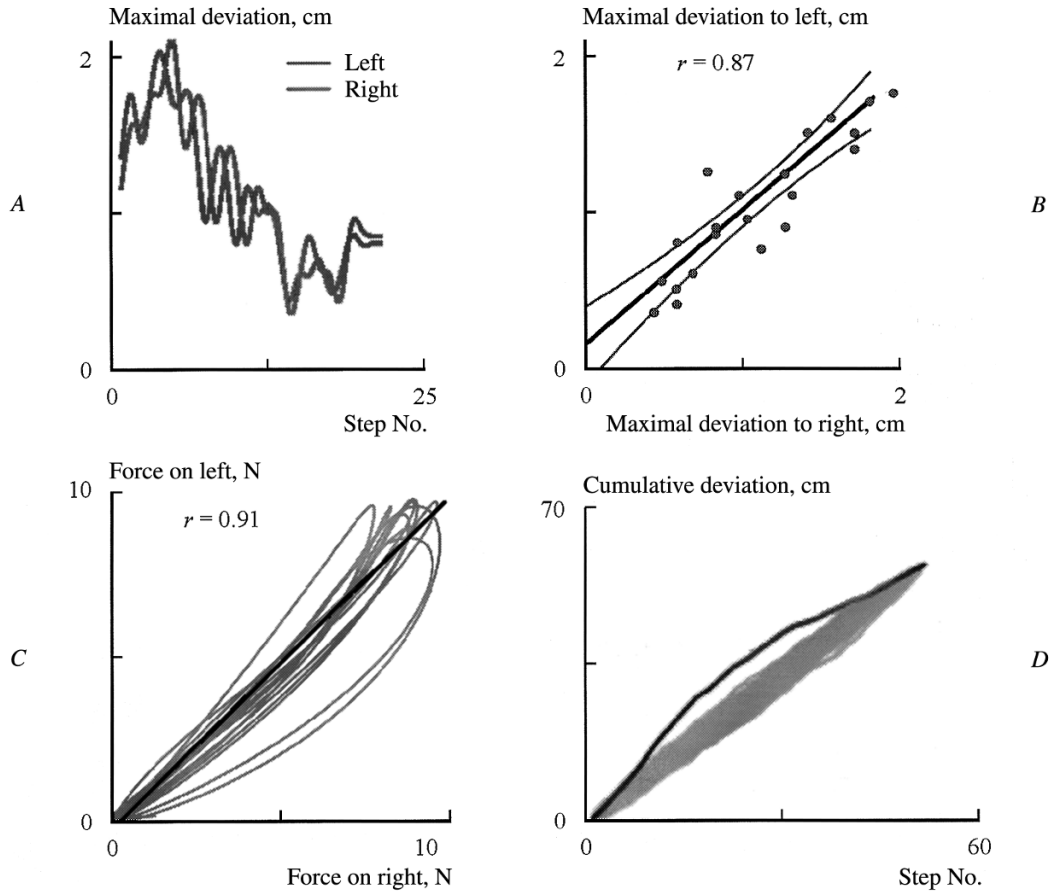

Fig. 2. Motor responses associated with dynamic destabilization on walking in decerebrate cats. *A*) Sequence of lateral deviations of the trunk from step to step, identifying a tight relationship between left and right motor responses, which gradually increased with subsequent progressive decreases over a number of uninterrupted steps; *B*) correlation between deviation of the trunk to the left and right and *C*) supporting force responses beneath the left and right paws; *D*) cumulative deviations of the trunk to the left and right in a decerebrate cat, plotted in order of appearance (black line) or randomized (Monte Carlo = 500, gray line). Displacement of the trunk to the left and right on walking falls out of the post-randomization range.

As shown in Fig. 2, *A*, the maximum lateral deviation of the trunk to the left and right were tightly linked from step to step. There was a gradual increase in the amplitude of deviations to the left and right, followed by a subsequent progressive decrease over a sequence of continuous steps. There was a quite high level of correlation between trunk deviations (Fig. 2, *B*). Force responses beneath the left paw of decerebrate cats also correlated closely with right paw forces (Fig. 2, *C*). Furthermore, the amplitude and duration of supporting force reactions, like hindlimb muscle activity, was strongly dependent on deviations of the body (Fig. 5, *A*). A high correlation (Fig. 5, *B*) was seen between force reactions and lateral deviations of the trunk ($p < 0.05$, $n = 4$, $r = 0.74 \pm 0.1$), though correlation coefficients were rather lower than those in intact animals ($p < 0.05$, $n = 4$, $r = 0.93 \pm 0.02$).

Detailed analysis of correlations between muscle activity and the kinetics and kinematics of the trunk and hindlimbs showed that each subsequent balance-correcting movement of the limbs depended on the preceding deviation of the trunk from the balance condition and prepared the subsequent locomotor cycle (Fig. 2). This is probably why effective maintenance of balance was achieved during walking with the center of gravity changing from second to second, requiring dynamic adaptation of the locomotor pattern. Figure 2, *D* shows that cumulative left and right deviations of the trunk in decerebrate cats, plotted in the order of their appearance (black line) during walking sequentially fell outside the range obtained after randomization (gray area) by the Monte Carlo method [12]. This provides an additional argument supporting the view that maintenance of balance is not affected by the magnitudes of responses on the left and right sides, but that balance is determined by the high correlation between preceding and subsequent motor reactions. These facts may constitute evidence supporting the notion that regulation is via feedback combined with the dynamic feedforward process underlying the control of bal-

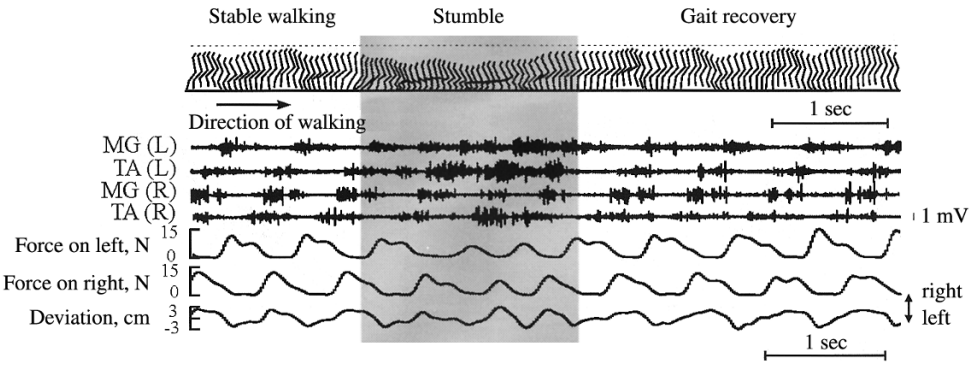

Fig. 3. Recovery of balance after stumbling during walking in a decerebrate cat. The plots show gait kinematics, myographic responses of extensors (MG (L and R) – gastrocnemius medialis, left and right), flexors (TA (L and R) – tibialis anterior, left and right), supporting force reactions bilaterally, and deviation of the trunk laterally before, during, and after stumbling.

ance during walking. Activation of the neural networks of the brainstem and spinal cord responsible for generating the motor pattern for the ongoing step determines the motor command which will be executed in the next step. In addition to the maintenance of balance in calm walking, the animal could independently restore balance during tests using perturbations (tilting of the support, lateral pushes to the pelvis), as well as during spontaneous stumbles, by redistributing muscle activity and altering the reciprocal relationships between them during the stepping cycle and modulating supporting force reactions (Fig. 3).

We then performed a comparative analysis of posture-correcting reactions in standing and active movement. Mesencephalic animals were placed on the treadmill tilted sideways (Fig. 1, *A*). Postural reactions were studied in cats fixed at the pelvis during standing and walking. Even without additional stimulation, tilting of the support (to the right) activated the contralateral extensors (on the left) which was clearly due to a reflex to stretching of the extensor muscles of the contralateral side in the flexed position [34]. Stimulation of the spinal cord significantly increased postural responses in standing cats (Fig. 4, *A*). Walking initiated by epidural stimulation demonstrated not only a consistent left-right redistribution of extensor activity, but also modification of a number of gait characteristics (Fig. 4, *B*): the amplitude and duration of EMG volleys and intervolley intervals [3] changed, with corresponding modulation of supporting force reactions and the durations of the phases of the locomotor cycle.

The final part of the experiments addressed postural capacity during walking after complete transection of the spinal cord. For several hours after spinal lesions, spinal cats showed stepping-on-the-spot movements, along with episodes of locomotor behavior with balance control on the moving treadmill in conditions of tonic electrical stimulation of the spinal cord and sensory mechanical stimulation in the tail area (Fig. 5, *A*). As with decerebrate cats, motor responses in spinal cats correlated with deviations of the body and were sufficient to correct balance. However, the effectiveness of these postural corrections ($p < 0.05$, $n = 4$, $r = 0.54 \pm 0.1$), muscle tone (Fig. 5, *B*), and supporting force reactions (Fig 5, *C*) were significantly smaller than in animals with the spinal cord intact. The result was that locomotion was less stable than in decerebrate cats and balance could not be recovered after stumbling and perturbations.

Discussion

Maintenance of body posture is a vitally important motor function. Effective control of the main body posture is just as important for standing and locomotion [19, 25, 37] as it is for performing voluntary movements. Postural regulation is mediated by a highly integrated, multisensory, hierarchically organized system [2, 8, 38]. Most motor and sensory centers of the CNS are involved in postural control, and impairment of any of the components of these postural control systems may lead to severe consequences for postural stability [24, 26, 28, 39].

The studies reported here showed that the spinal cord, brainstem, and cerebellar motor system in decerebrate animals, using only somatosensory signals from the limbs, can provide basal control of posture and balance. Experiments using different levels of brainstem transection in cats provide support for results obtained previously in decerebrate rabbits [32]. Animals decerebrated at the rostral levels (precollicular-premammillary) were found to be able to stand and walk spontaneously with the body weight supported. The overall configuration of body posture, righting adjustment reflexes, and the distribution of limb muscle tone were close to normal. Postural responses to the tilted platform were not fundamentally different from the responses of intact animals but had lower amplitude and were slower. A cyclical dynamic was seen: periods of decreased activity and muscle tone alternated with periods of increased activity and spontaneous locomotion. More caudally decerebrated (precollicular-postmammillary, intercollicular) animals

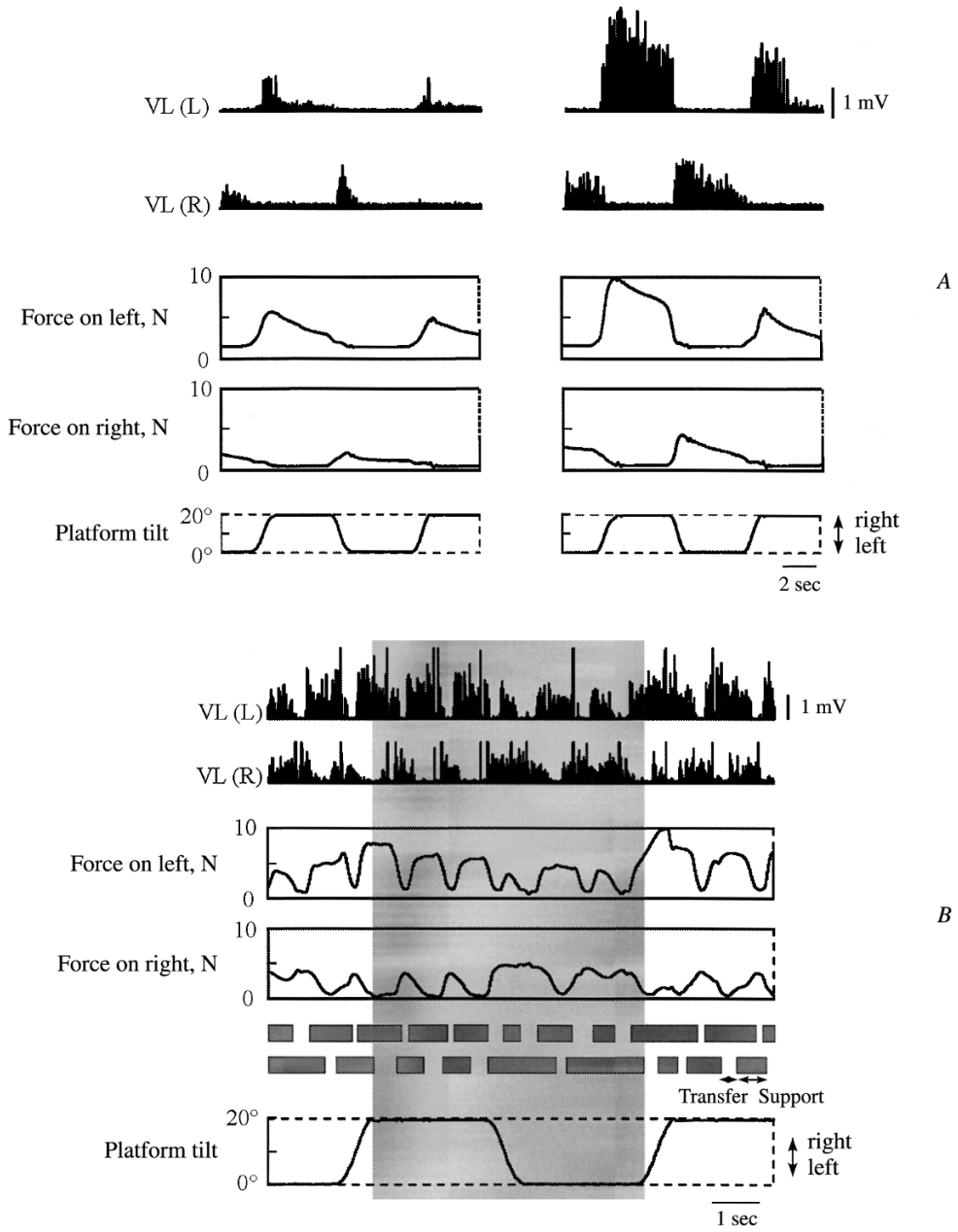

Fig. 4. Postural reactions on tilting the support in a decerebrate cat during walking and standing. *A*) Myographic responses in the extensors (VL (L and R) = vastus lateralis, left and right), supporting force reactions bilaterally in a decerebrate cat with the pelvis fixed during standing before (left) and after (right) epidural stimulation of the spinal cord; *B*) during locomotion initiated by epidural stimulation.

were characterized by decreased muscle tone and were unable to maintain balance or righting reflexes. However, stimulation of the ventral tegmental field and the mesencephalic locomotor region increased muscle tone and the ability to perform postural corrections. Stimulation of the mesencephalic locomotor region at higher amplitude also led to quadripedal locomotion. Comparison of the postural capacities of animals decerebrated at different levels, the effects of stimulation of the motor nuclei in these animals, and macroscopic and microscopic studies of the brainstem below the level of transection suggested that neural centers such as the nucleus ruber, the nucleus raphe magnus, and the nucleus cuneiformis have an important role in postural control [30, 32]. The substantia nigra evidently has key importance in the brainstem regulation of the main body posture, as stem transections damaging this structure caused

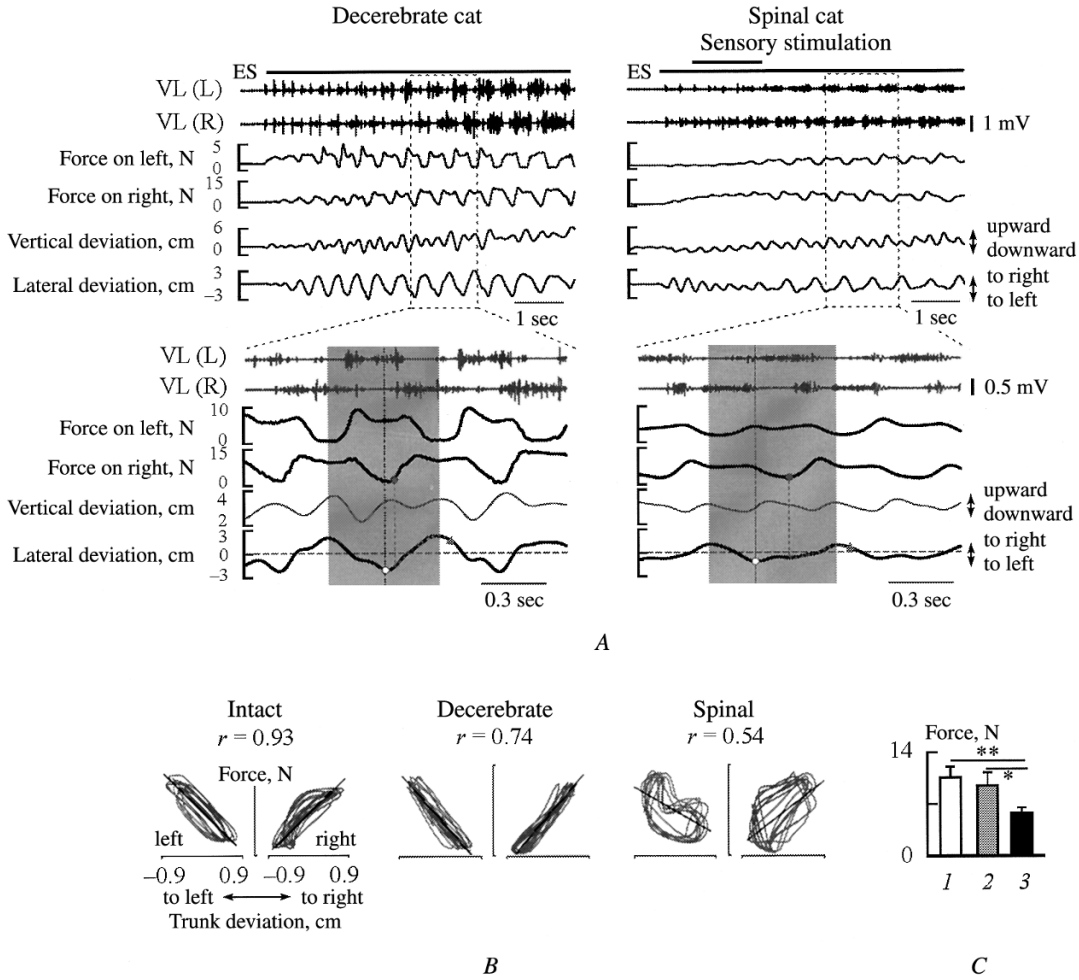

Fig. 5. Walking with maintenance of body weight in decerebrate and spinal cats. *A*) Myographic responses in extensors (VL (L and R)), supporting force reactions bilaterally, and vertical and lateral deviations of the trunk in a decerebrate and a spinal cat in acute experiments with bipedal hindlimb walking initiated by epidural (ES) and sensory stimulation; *B*) correlation between left-right force responses and deviations of the trunk (n = 10–15 steps in each group); *C*) mean amplitude of supporting force responses during walking in intact (*1*), decerebrate (*2*), and spinal (*3*) cats (n = 4 in each group, 10–15 steps for each cat). Significant differences between groups: $^{*}p < 0.05$, $^{**}p < 0.01$.

complete loss of the animals' ability to perform adjusting reflexes [26] and maintain balance independently.

Postural control has been addressed in many reports [6, 7, 10, 25, 32], performed in a variety of animal models in standing. During standing, the state of balance was rapidly recovered in response to perturbing influences in both decerebrate and intact animals as a result of postural corrections. Recent years have seen the publication of a number of studies of postural reactions during walking [29, 35] showing that execution of locomotor tasks also requires effective maintenance of posture and balance. The present experiments addressed postural regulation during active movement and differences from posture control on standing. The data obtained here provide evidence that the central apparatus in decerebrate animals, which lack a forebrain, effectively controls body posture in both standing and walking. However, different reflex mechanisms were used. Tilting of the support for standing cats induced right-left redistribution of extensor muscle activity. Postural correction in response to tilting of the treadmill during walking also induced the corresponding changes in the dynamic properties of the motor pattern, the amplitude-time characteristics of locomotor EMG volleys, and the durations of the swing and transfer phases. Similar conclusions on differences in the mechanisms controlling lateral stability in standing and walking were obtained previously in experiments on intact cats [21, 22].

Detailed analysis of kinematic data showed that dynamic balance is also actively controlled in decerebrate cats during calm locomotion, when no additional perturbing influence was used. The cats' trunks deviated to the side during the stepping rhythm. Despite this regular destabi-

lization of the center of gravity, the animals did not fall, but the amplitudes of left and right lateral deviations also correlated (Fig. 2) with supporting force reactions (Fig. 5). In addition, there was a close interaction between body deviations and lateral paw positioning and step width, as demonstrated previously [35]. Dynamic corrections of the mediolateral position of the foot during the support phase and the amplitude of supporting force reactions, reciprocality between the flexor and extensor mechanisms, and changes in the activity of the abductor and adductor muscles provided effective compensation for lateral deviations of the trunk. Comparison of intact and decerebrate animals [35] demonstrated similarity in the postural mechanisms before and after decerebration, which is evidence that the brainstem and spinal cord are of key importance in the motor control of body posture and balance.

Posture is maintained mostly via innate reflex mechanisms [10, 28]. On the one hand, the spinal cord is a conductor for supraspinal posture-correcting commands; on the other hand, it contains its own intrinsic postural reflex mechanisms responsible for postural correction. The relative importance of these two functions of the spinal cord is not understood. It is well known that animals with complete spinal transection at the lower thoracic level cannot maintain the balance of the posterior part of the body [25], though reduced postural reactions can persist and show some improvement with training [11]. These are different ways of interpreting these results. On the one hand, they can be regarded as evidence for the minimal contribution of spinal postural reflexes to maintaining balance [19]. An alternative hypothesis is that transection of the spinal cord deprives the spinal postural mechanisms of the required tonic supraspinal influences, with the result that they are in the inactive state [10, 24].

Impairment to supraspinal control has different effects on locomotor and postural functions. While the spinal motor system deprived of influences from the brain can generate rhythmic locomotor movements [11], previous studies did not show whether spinal animals have sufficient postural ability to maintain balance [19, 25]. The general view is therefore that the spinal apparatus contains neural networks able to generate a rhythmic locomotor pattern, while maintenance of dynamic balance requires the involvement of brainstem centers and forebrain [10, 25]. However, our recent studies showed that the postural capacities of spinal animals can be activated by external influences [34]. Spinal rabbit preparations cannot maintain posture independently, though postural reflexes could be enhanced by electrical and pharmacological stimulation of the spinal cord. This is evidence that the basal mechanisms of postural reactions are mediated at the level of the spinal cord, while the descending projections from the higher neural centers activate spinal reflex networks and control their operation allowing for vestibular, visual, somatosensory, and other information.

The experiments reported here on decerebrate and spinal cats showed that spinal networks receiving only the somatosensory afferent input from the limbs were also able to maintain balance during locomotion if these networks were activated by nonspecific tonic signals. Consequently, suppression of the postural capacities after impairment of supraspinal control is probably due to decreased excitability of the spinal networks than the inability of these networks to produce correct responses to somatosensory signals associated with maintenance of balance during standing and walking. These data provide experimental support for recent model studies [23], showing that sensorimotor control of balance during complex multiple-joint motor acts in mammals can be mediated on the basis of a simple and plastic feedback strategy at the level of the spinal cord and brainstem, not involving higher levels of CNS control.

Performance of these and other postural tasks during locomotion and even free walking with second-by-second changes in the position of the center of gravity requires dynamic adaptation of the locomotor pattern [18]. The present experiments using a decerebrate model yielded data suggesting that this adaptation occurs not only in response to disturbances to the state of balance (by the feedback control mechanism), but also by a feedforward mechanism, preparing the following locomotor cycle. The study results suggest that the neural networks of the brain and spinal cord are supported by the mechanisms of short-term memory of immediately preceding sensory and motor events and use these engrams in planning and executing subsequent movements linked with maintenance of balance during walking [17]. The neural mechanisms operating in the complex physiological phenomena of the integration of the locomotor and postural systems at the level of the spinal cord and brainstem require further study. Apart from its basic importance, this may be of value in developing more effective mechanisms for activating the spinal neural networks playing the key role in posture control [33] and open up new perspectives for motor rehabilitation of patients with spinal cord lesions.

This study was supported by the Russian Foundation for Basic Research (Grant Nos. 11-04-01669-a, 11-04-12073-ofi-m-2011, and 11-04-12074-ofi-m-2011) and a grant from the President of the Russian Federation (MK-5684.2012.4). The study was supported by the "Molecular mechanisms of physiological functions" Basic Studies Program of the Presidium of the Russian Academy of Sciences.

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