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Research report

Postural performance in decerebrated rabbit

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Abstract

It is known that animals decerebrated at the premammillary level are capable of standing and walking without losing balance, in contrast to postmammillary ones which do not exhibit such behavior. The main goals of the present study were, first, to characterize the postural performance in premammillary rabbits, and, second, to activate the postural system in postmammillary ones by brainstem stimulation. For evaluation of postural capacity of decerebrated rabbits, motor and EMG responses to lateral tilts of the supporting platform and to lateral pushes were recorded before and after decerebration. In addition, the righting behavior (i.e., standing up from the lying position) was video recorded.

We found that, in premammillary rabbits, responses to lateral tilts and pushes were similar to those observed in intact ones, but the magnitude of responses was reduced. During righting, premammillary rabbits assumed the normal position slower than intact ones.

To activate the postural system in postmammillary rabbits, we stimulated electrically two brainstem structures, the mesencephalic locomotor region (MLR) and the ventral tegmental field (VTF). The MLR stimulation (prior to elicitation of locomotion) and the VTF stimulation caused an increase of the tone of hindlimb extensors, and enhanced their responses to lateral tilts and to pushes.

These results indicate that the basic mechanisms for maintenance of body posture and equilibrium during standing are present in decerebrated animals. They are active in the premammillary rabbits but need to be activated in the postmammillary ones.

Keywords: Posture; Balance; Sensory–motor integration; Decerebrated rabbit; Mesencephalic locomotor region; Ventral tegmental field

1. Introduction

In quadrupeds, the most common posture of the body, with its dorsal side oriented upward (basic posture), is maintained by the postural system. This closed-loop control system is driven by sensory feedback signals and compensates for deviations from the desired body orientation by producing corrective motor responses (for review see [5,11,21,22]).

Many motor centers, from the spinal cord to the motor cortex, seem to participate in the maintenance of body posture [11,13]. However, the distribution of postural functions between these centers and the specific role of each of them in the control of posture are not quite clear [17,18]. Nevertheless, one principal fact is well established—the animals (cats and rabbits) with more rostral decerebration are capable of standing and walking without losing balance [1,19]. This fact implies that a substantial part of the system controlling body posture and equilibrium is located below the decerebration level, that is, in the brainstem, cerebellum, and spinal cord.

The capacity of decerebrated animals to maintain equilibrium, that is, to react properly to different perturbations of posture, has not been systematically investigated, however. This issue was addressed in the present study with experiments on rabbits. We used this animal model because (i) the rabbit does not need special training for the postural task of keeping balance on the tilting platform, and (ii) the functional organization of postural control system in the rabbit was characterized in our previous studies [1].

The first specific aim of the present study was to characterize postural performance in the decerebrated rabbits. Since the level of decerebration is known to strongly affect the animal's motor activity including the value of muscle tone, the intensity of reflex responses, and the spontaneous movements (see e.g., [1,28]), we examined postural performance in animals decerebrated at different rostro-caudal levels, premammillary and postmammillary ones (see below).

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It is known that in intact quadrupeds, a lateral tilt of the supporting surface causes corrective movements, which restore the dorsal side up orientation of the trunk. The functional organization of the postural control system generating these corrective movements in rabbits and cats has been analyzed in our previous studies [2,4]. It was found that this system consists of two relatively independent sub-systems responsible for stabilization of the anterior and posterior part of the trunk, respectively. Each of the sub-systems is driven by somatosensory input from the limbs of the corresponding girdle. In the present study, we evaluated operation of the hindlimb sub-system in decerebrated rabbits. For this purpose, we compared the motor and EMG responses to lateral tilts of the platform supporting the hindquarters before and after decerebration.

An important postural task is compensation for trunk displacements in the frontal plane caused by a lateral force applied to the body. Intact quadrupeds, when standing, easily correct for lateral pushes and do not fall even with application of rather large forces [16]. Recently, operation of the postural mechanisms of the hind- and forequarters in response to application of pushes to the posterior or to the anterior part of the trunk was examined in cats [15]. In the present study, we evaluated operation of the hindquarters mechanism of this system by comparing motor and EMG responses to lateral pushes in rabbits before and after decerebration.

When positioned on their side, quadrupeds exhibit a set of righting reflexes and rapidly assume the basic standing posture [19]. In the present study, we compared the capacity to stand up from the lying position in the rabbits before and after decerebration.

The postural control system usually interacts with other motor systems. In particular, it provides postural support for voluntary movements of the trunk and limbs [23]. Another important function of the postural system is maintenance of equilibrium at the onset of and during locomotion [25,29]. *The second specific aim* of the present study was to examine the effect of activation of the locomotor system on the postural system. For this purpose, we characterized the effects of electrical stimulation of the mesencephalic locomotor region (MLR) [14,31] on postural performance in the postmammillary rabbits.

An important condition for postural activity is sufficient tone of the antigravity (extensor) muscles (see e.g., [7,25]). An increase of the extensor tone in decerebrated animals can be caused by stimulation of the ventral tegmental field (VTF) in the medial brainstem [26]. *The third specific aim* of this study was to examine the effect of VTF stimulation on muscle tone and on the capacity to perform postural corrections in the postmammillary rabbits.

A brief account of part of this study has been published in abstract form [27].

2. Methods

2.1. Subjects

Experiments were carried out on 15 adult male New Zealand rabbits (weighting 2.5–3.0 kg). All experiments were conducted with the approval of the local ethical committee (Norra Djurforsoksetiska Namnden) in Stockholm.

2.2. Surgical procedures

Each animal was subjected to two surgeries. First, under Hypnorm-midazolam anesthesia, using aseptic procedures, bipolar EMG electrodes (0.2 mm flexible stainless steel Teflon-insulated wires) were implanted bilaterally into *M. gastrocnemius* (Gast, ankle extensor) and *M. vastus* (Vast, knee extensor). The wires were led sub-cutaneously toward the head and then through a small incision in the skin on the dorsal aspect of the neck. The wound was sutured so that the wires were fastened to the skin. A small connector was soldered to each wire at a distance of 2–3 cm from the skin.

In 1–2 days, when the animal had recovered completely from the first surgery, its postural capacity was tested (see below), and then the second surgery was performed. The animal was injected with propofol (average dose 10 mg/kg i.v.) for induction of anesthesia, which was continued on isoflurane (1.5–2.5%) delivered in O_2. The trachea was cannulated. The animal was then decerebrated. The scalpel entered the brainstem at the precollicular level, but the angle of cutting varied between different subjects. In Fig. 1A, all transections made in the present study are divided into two categories, the premammillary ones (1) and postmammillary ones (2), strongly differing in their effect on postural performance (see below). After decerebration, the anesthesia was discontinued. During the experiment, the rectal temperature and mean blood pressure of the animal were continuously monitored and were kept at 37–38 °C and at greater than 90 mmHg, respectively. Recordings in decerebrated animals were started no less than 1 h after cessation of anesthesia.

2.3. Experimental design

Two types of experiments were carried out on decerebrated rabbits. *First*, the animals were not restrained (Fig. 2A). The hindlimbs were standing on the tilting platform (P), whereas the forelimbs had a stationary position. *Second*, to stimulate brainstem structures (MLR and VTF), the animals were restrained by fixing the head in a stereotaxic device (Fig. 2B). The hindlimbs were standing on the tilting platform, whereas the forequarters were suspended.

In both types of experiments, two tests for postural reactions during standing were used: lateral tilts and lateral pushes. The tilts of the platform had a peak-to-peak value of 40° (Fig. 2D). Two types of tilt trajectories were used: a sine-like trajectory (Fig. 9B) with a frequency of 1 Hz, and a trapezoidal trajectory (Figs. 5A, B, 7 and 9D) with transition between stationary (extreme) positions taking 0.5–1.5 s and with each position being maintained for 1.5–3 s. In both sinusoidal and trapezoidal tests, tilts were symmetrical in relation to the horizontal position.

Lateral pushes were applied in the medial-lateral direction to the trunk in the lumbar region (Fig. 2E) using a pusher (cylindrical tool 1.5 cm in diameter and 10 cm in length) with a force sensor on the side facing the rabbit. This sensor was used to characterize timing of push application. Each push lasted for 150–200 ms. During the push, an experimenter displaced the trunk by a few centimeters in the medio-lateral direction, after which the pusher was rapidly withdrawn.

A mechanical sensor (S), positioned at a half-height of the caudal part of the body (Fig. 2), measured lateral displacements of this body area in relation to the supporting platform. These displacements allowed characterizing postural corrections generated in response to lateral pushes; in unrestrained animals they show postural corrections caused by platform tilts (Fig. 2D) [2]. The EMGs of hindlimb muscles were recorded during postural tests along with the data from the mechanical sensors.

To characterize the body configuration of the standing rabbit, the side view and view from below (using a transparent horizontal platform and a mirror) were simultaneously video recorded (25 frames/s). To characterize the righting behavior, the rabbit was positioned on its side by the experimenter and then released. The sequence of movements aimed at assuming the standing posture was video recorded. In addition, a sequence of locomotor movements was video recorded.

The intact rabbits, intended for decerebration, were used as controls. Before decerebration, they were tested (by lateral tilts and pushes) in the non-restrained condition. In addition, the basic body configuration and righting were video recorded.