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NEURAL MECHANISMS OF SINGLE CORRECTIVE STEPS EVOKED IN THE STANDING RABBIT

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Abstract—Single steps in different directions are often used for postural corrections. However, our knowledge about the neural mechanisms underlying their generation is scarce. This study was aimed to characterize the corrective steps generated in response to disturbances of the basic body configuration caused by forward, backward or outward displacement of the hindlimb, as well as to reveal location in the CNS of the corrective step generating mechanisms. Video recording of the motor response to translation of the supporting surface under the hindlimb along with contact forces and activity of back and limb muscles was performed in freely standing intact and in fixed postmammillary rabbits. In intact rabbits, displacement of the hindlimb in any direction caused a lateral trunk movement toward the contralateral hindlimb, and then a corrective step in the direction opposite to the initial displacement. The time difference between onsets of these two events varied considerably. The EMG pattern in the supporting hindlimb was similar for all directions of corrective steps. It caused the increase in the limb stiffness. EMG pattern in the stepping limb differed in steps with different directions. In postmammillary rabbits the corrective stepping movements, as well as EMG patterns in both stepping and standing hindlimbs were similar to those observed in intact rabbits. This study demonstrates that the corrective trunk and limb movements are generated by separate mechanisms activated by sensory signals from the deviated limb. The neuronal networks generating postural corrective steps reside in the brainstem, cerebellum, and spinal cord.

Key words: corrective steps, muscle synergy, postural control, rabbit, sensory feedback.

INTRODUCTION

When standing, bipeds and quadrupeds maintain a specific basic body posture (the body orientation in space and the body configuration) due to activity of the postural control system. This system is driven by sensory feedback signals and generates corrective motor responses when the body posture deviates from the desired one (for review, see Horak and Macpherson, 1996; Massion, 1998; Deliagina et al., 2012, 2014). Both bipeds and quadrupeds use different strategies to stabilize the body orientation when standing. These strategies depend on the type and strength of postural perturbations, as well as on other factors. They could be divided into two groups: fixed-support strategies and change-in-support strategies (Horak, 2009; Maki and McIlroy, 1997). Fixed-support strategies include postural corrections caused by redistribution of the activity of the muscles which does not lead to a change of the support area. Change-in-support strategies include postural corrections resulting in a change of the support area, such as performing a corrective step or movement of the arm aimed to reach the support. It was found that the same types of postural perturbations (e.g. caused by tilt or translation of the support surface, by lateral push applied to the trunk) can evoke execution of the fixed-support strategy or the change-in-support strategy (the corrective step) (Beloozerova et al., 2003; Karayannidou et al., 2009). It was also shown that when the change-in-support strategy including the corrective step was generated in response to translation of the support surface in human, the functional muscle synergies characteristic for the fixed-support strategy were observed in the supporting limb (Chvatal et al., 2011; Burleigh et al., 1994).

It was suggested that change-in-support strategy is used when the fixed-support strategy is insufficient, and there is a risk of falling down (Horak and Nashner, 1986). However, later it was shown that in human, a corrective step could be initiated well before the moment when the center of mass appeared near the stability limits of the base of support (Maki and Whitelaw, 1993; Maki and McIlroy, 1997).

Fixed-support strategies executed in response to different types of postural perturbations were studied in considerable detail (Macpherson and Fung, 1999; Musienko et al., 2008, 2010; Honeycutt et al., 2009; Honeycutt and Nichols, 2010; Beloozerova et al., 2003; Deliagina et al., 2006, 2012; Karayannidou et al., 2008, 2009). By contrast, our knowledge about the operation of the postural systems generating change-in-support strategies, in particular those which include a corrective step, is extremely limited. It was shown that in humans, translation of the support surface in any particular direction evoked, first, the body weight shift toward one of the legs and then a corrective step performed by the unloaded limb in the direction opposite to the direction

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of the surface translation (Maki et al., 1996). It was also demonstrated that manipulation of sensory signals from receptors of the foot sole affected the probability of initiation of the corrective step (Perry et al., 2000).

Recently we found that distortion of the basic body configuration caused by displacement of the limb in the standing rabbit, evoked postural response restoring the initial body configuration (Hsu et al., 2014). This postural response included a single corrective step performed by the displaced limb in the direction opposite to the direction of the initial displacement while the other limbs remained standing. The goal of the present study was to analyze the neural mechanisms underlying the generation of postural responses to distortion of the basic standing body configuration caused by displacement of a single limb in different directions. For this purpose, *first*, these postural responses were characterized in details in intact standing rabbit. We found, that the limb displacement evoked a lateral movement of the trunk toward the contralateral (supporting) limb, and then a corrective step. During the corrective step the direction of the trunk movement was reversed and to the end of the step the body configuration returned to the initial one. *Second*, to determine the location in the CNS of the basic networks underlying generation of the postural response under the study, the motor response to displacement of the limb in relation to the trunk was examined in decerebrate premammillary and postmammillary rabbits. It was found that integrity of higher levels of CNS was not necessary for generation of the postural reaction to distortion of the basic body configuration.

A brief account of a part of this study has been published in abstract form (Hsu et al., 2014).

EXPERIMENTAL PROCEDURES

Experiments were carried out on 16 adult New Zealand rabbits (weight 2.5–3.5 kg). All experiments were conducted with approval of the local ethics committee (Norra Djurförsöksetiska Nämden) in Stockholm.

Surgical procedures

All animals were subjected to a surgery performed under Hypnorm-midazolam anesthesia, using aseptic procedures. Bipolar EMG electrodes (0.2-mm flexible stainless steel Teflon-insulated wires) were implanted bilaterally into four selected muscles of the trunk and/or hindlimbs. The recorded muscles, as well as the number of animals in which individual muscles were recorded, are listed in Table 1. The wires were led subcutaneously 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 surgery, it was subjected to postural tests (see below). After few days of testing, seven animals were taken to acute experiment. The animal was injected with propofol (average dose 10 mg kg-1 i.v.) for induction of anesthesia, which was continued on isoflurane (1.5–2.5%) delivered in O_2. The trachea was cannulated. For all subsequent procedures, six animals were positioned in a metal frame, and its head and vertebral column were rigidly fixed (Fig. 1G). Then they were decerebrated at the precollicular-postmammillary level (Musienko et al., 2008). One animal was decerebrated at the precollicular-premammillary level (Musienko et al., 2008) without the body fixation. 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. The experiments were terminated by a lethal dose of anesthetic (pentobarbital sodium).

Table 1. Recorded muscles and their function

Muscle	Abbreviation	Function	*N*
Sartorius	Sart	Hip flexor	3
Adductor longus	*Add*	Hip adductor	2
Gracilis	Grac	Hip extensor and adductor	3
Gluteus medius	Glut	Hip extensor and abductor	3
Abductor cruris caudalis	*Abd*	Caudal abductor of shin	3
Rectus femoris	(RF)	Hip flexor and knee extensor	2
Vastus medialis	*Vast*	Knee extensor	4
Bicep femoris	Bic	Hip extensor and knee flexor	3
Semimembranosus	Sm	Hip extensor and knee flexor	3
Semitendinosus	(St)	Hip extensor and knee flexor	4
Tibialis anterior	Tib	Ankle flexor	10
Extensor digitorum longus	EDL	Ankle flexor and extensor of digits	2
Gastrocnemius	(Gast)	Ankle extensor	4
Oblique externus abdominis	OEA	Ipsilateral bending and contralateral twisting of the spine	2
Erector spinae	ES	Ipsilateral bending and contralateral twisting of the spine	3
Multifidus	MF	Ipsilateral bending and contralateral twisting of the spine	3

In Abbreviation column, parenthesis indicate that the muscle was not active in the standing limb, italic indicates that the phase of the muscle activity in the stepping limb varied in different animals, underline indicates that the phase of the muscle activity in the standing limb varied in different animals. *N*, the number of animals in which a particular muscle was recorded.

Experimental design

Experiments on intact rabbits and on premammillary rabbit. No special training of the animal was performed prior to postural testing. During the test, the animal was freely standing on four horizontal platforms (Fig. 1A–C). A movable thin plastic plate (23 × 10 × 0.3 cm) with