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Variety of muscle responses to tactile stimuli

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Abstract. Influences exerted by tactile stimuli on the muscle activity were investigated with two methods: (1) analysis of kinematics and electromyographic (EMG) activity of eight forelimb muscles during contact placing (CP) reactions elicited by tactile stimuli applied to the dorsal, medial or lateral sides of the paw in cats, and (2) the Hoffmann (H) - reflex technique to quantify the effects of the tactile stimuli on the excitability of the alpha motoneurones of the soleus muscle in awake rats. The first group of the data showed that the tactile stimuli applied to dorsal, medial or lateral aspects of the paw led to different strategies of the forelimb movements during CP reactions. These differences arose from various patterns of activation of the elbow flexor and extensor muscles at the beginning of CP reactions and a various involvement of the medio-lateral components of movements, depending on the site of the tactile stimulus application. With the H-reflex technique it was found that the tactile stimulus diminished the excitability of alpha motoneurones of the soleus muscle when applied to the skin overlying the lateral side of the ankle joint. This effect was in line with the observation that the tactile stimulus applied to the lateral side of the paw activated the elbow flexor muscles but not their antagonists to initiate CP reaction.

Review

Key words: contact placing, forelimb movements, limb muscles, H-reflex, cutaneous input

INTRODUCTION

It is generally accepted that the tactile stimulus applied to various aspects of extremities exerts excitatory effects on the motoneurones innervating the flexor muscles (Baldissera et al. 1980). There are, however, some exceptions e.g., the palmar aspect of the paw and the foot, the anal area and the inner thigh. The touch or light pressure of these areas activates the extensor muscles (Sherrington 1910, Engberg 1964, Barbeau and Rossignol 1987). Also Hagbarth (1952) showed that strong tactile stimuli exerted excitatory effects on the extensor motoneurones when the stimulus was applied to the skin area overlying the extensor muscles. All these data indicate that excitatory effects exerted by the tactile stimuli on the extensor motoneurones are not quite exceptional. Our data on the postural reactions of the contact placing give an example that the tactile stimulus might activate the extensor and/or the flexor muscles, depending on the site of the stimulus on the paw (Czarkowska-Bauch et al. 1993, Czarkowska-Bauch 1996, in press).

CONTACT PLACING REACTIONS IN THE CAT

Contact placing (CP) reactions belong to the basic repertory of postural reactions in mammals and they are widely used to correct a posture when the extremity unexpectedly meets an obstacle, e. g., during stumbling (Bard 1933). The reactions are elicited by light tactile stimuli applied to the distal part of an unsupported limb. This induces the placement of this limb on the touching object (Bard 1933). CP reaction consists of two phases: (1) a withdrawal of the limb from the touching object, and (2) a placing of the limb on this object.

The receptive field of CP reactions is located at the most distal parts of the forelimb. The reactions are elicited the most regularly (in over 90% of trials) to stimulation of these areas (Czarkowska-Bauch 1990). A frequency of eliciting CP reactions decreases proximally so that they are obtained only in about 25% of trials when the stimulus is applied to the skin over the elbow joint (see Fig. 1 in Czarkowska-Bauch 1990). The reaction times (i.e., the interval between the onset of the tactile stimulation and the time of the contact of the paw with the "landing" plate of the stimulating apparatus) ranged between 310 ms and 475 ms when lateral side of the paw was stimulated (lateral CPs), from 305 ms to 538 ms in the medial and between 310 ms and 524 ms in the dorsal CPs (individual median values) (Czarkowska--Bauch 1990, Czarkowska-Bauch 1996, in press). The reaction times increased when more proximal skin areas were stimulated (Czarkowska-Bauch 1990).

Activity of the forelimb muscles during dorsal, medial and lateral contact placing reactions

The location of the tactile stimulus on the dorsal, medial or lateral side of the paw influenced the pattern of activation of the elbow flexor and extensor muscles (Czarkowska-Bauch 1990; Czarkowska--Bauch et al. 1993, Czarkowska-Bauch 1996, in press). In all the reactions the elbow flexor muscles (particularly biceps brachii - Bi) were activated with the shortest latencies (Czarkowska-Bauch et al. 1988, Czarkowska-Bauch 1990, Czarkowska-Bauch et al. 1993). However, in the majority of dorsal and in about 50% of the medial CP reactions the onset of the tactile stimulation activated also the elbow extensor muscles with similar latencies (Czarkowska--Bauch et al. 1993). Further analysis showed that the elbow flexor and extensor muscles were very frequently coactivated at the beginning of the dorsal and in about 50% of the medial CP reactions. The co-contraction of the elbow flexor and extensor muscles presumably locked the elbow joint at the beginning of the reaction and delayed its flexion (Czarkowska-Bauch 1990). In contrast, during lateral CP mainly the elbow flexors but not their antagonists were activated at the beginning of a withdrawal phase. Thus, in the lateral CP the movements started with a flexion at the elbow (Czarkowska-Bauch et al. 1993, Czarkowska-Bauch 1996, in press).

Muscles acting at the wrist and digits were also activated in a different way depending on the location of the tactile stimuli. Stimulation of the dorsal and medial aspects of the paw activated, with the shortest latencies, the extensor carpi ulnaris (ECU). This early activity contributed to the initiation of a lateral deviation of the paw at the beginning of a withdrawal phase (Czarkowska-Bauch 1990). Also flexor carpi ulnaris and radialis (FCU and FCR) were activated with short latencies to produce a palmar flexion of the wrist at the beginning of the reaction (Czarkowska-Bauch 1990). In contrast, when the stimulus was applied to the lateral side of the paw it activated mainly FCR muscle. Both ECU and FCU muscles were activated much less frequently at the beginning of the reaction (Czarkowska-Bauch 1996, in press).

Movement of the forelimb during contact placing reactions

Various patterns of the muscles activity led to different kinematics during dorsal, medial and lateral CP reactions. Both during dorsal and medial CP reactions a withdrawal phase was initiated by a backward and upward movement of the limb accompanied by a palmar flexion and lateral (ulnar) deviation of the paw (Czarkowska-Bauch 1990, Czarkowska-Bauch 1996, in press). In these two reactions the elbow flexion movement developed with a delay. In contrast, during lateral CP reactions the elbow flexion movement initiated the reaction together with a backward and upward displacement of the limb associated with a medial (radial) deviation and a palmar flexion of the paw (Czarkowska-Bauch 1996, in press).

A placing phase started in all the reactions at the distal joints with a dorsiflexion of the paw (Czarkowska-Bauch 1990, Czarkowska-Bauch 1996, in press). It was followed by the elbow extension movement which appeared with a very short delay in the lateral CPs but with a long delay in the dorsal and medial CP reactions. A downward movement of the limb appeared usually during the last 30% of the reaction times. The other striking difference between movements of the forelimb during dorsal, medial and lateral CP reactions was a various involvement of the medio-lateral components. Both in the medial and dorsal CPs, an abduction of the arm was associated mainly with a withdrawal of the limb while an adduction accompanied the sequence of movements leading to the placing of the limb on the apparatus (Czarkowska-Bauch 1990, Czarkowska-Bauch 1996, in press). However, during medial CPs an abduction and adduction of the arm occupied a similar percentage of the reaction time while in the dorsal CP the abduction lasted three times longer than adduction of the arm. Moreover, in the medial CPs the adduction of the arm initiated the sequence of movements at the proximal joints which led to the placing of the limb on the apparatus whereas in the dorsal CPs it was involved in a later period of the reaction. In contrast, during lateral CP the abduction of the arm occupied almost 75% of the reaction time and accompanied the sequence of movements during a lifting phase as well as those leading to a placing of the limb on the apparatus (Czarkowska-Bauch 1996, in press). The adduction of the arm occupied only a few percentage of the reaction time at the beginning and at the end of the reaction.

Also at the wrist joint the medio-lateral components of the movement were involved in all CP reactions. A radial deviation of the paw appeared at the beginning of a withdrawal phase both in the lateral and dorsal CP reactions while an ulnar deviation appeared at the beginning of the medial CPs. The medio-lateral components of the movement at the distal joints were also involved in a placing phase of the reactions but their timing was different in dorsal, medial and lateral CPs (Czarkowska-Bauch 1990, Czarkowska-Bauch 1996, in press).

In conclusion, various patterns of muscle activity at the elbow and wrist joints as well as a different time-table of kinematic events during dorsal, medial and lateral CP reactions indicate that various strategies of movement were used in these reactions depending on the site of the tactile stimulation. In one of them, characteristic for the reactions elicited by the tactile stimulus applied to the dorsal side of the paw, a backward-upward movement at the proximal joints accompanied by a palmar flexion and ulnar deviation at the wrist joint initiated the reaction. The elbow flexion followed this sequence of movements with some delay. A similar strategy was observed in about 50% of the reactions elicited by stimulation of the medial side of the paw. The other strategy of movement was used when the reaction was elicited by the stimuli applied to the lateral side of the paw. Lateral CP was initiated with a powerful flexion at the elbow joint accompanied by a radial deviation of the paw. A backward-upward movement accompanied by an adduction of the arm appeared later.

The question arises whether different strategies of the movement in CP reactions evoked by the tactile stimulation of various surfaces of the paw are important when the animal has to overcome an obstacle? A strategy of the movement, which locks the elbow joint at the beginning of the dorsal CPs, allows the cat to withdraw the forelimb from the touching object easier than when the elbow flexion movement starts simultaneously with the movements at the proximal and distal joints. The early flexion at the elbow would bring the wrist joint closer to an obstacle. Thus, a bigger movement at the proximal and distal joints would be required to compensate it.

It is clear that when an obstacle appears at the lateral side of the forelimb, an early elbow flexion does not interfere with the obstacle. Indeed, the elbow flexion together with a medial deviation of the paw and adduction of the arm allows the cat to withdraw the limb efficiently from a touching object. Such a strategy was used during lateral CP reactions.

Previously, Forssberg (1974, 1979) attributed differences between medial, lateral and dorsal CP reactions to the differential involvement of the abductor and adductor motoneurones during these reactions. However, our observations indicate that the differences between them are much more profound and complex. The tactile stimuli applied to various aspects of the paw totally changed both the timing and the pattern of activation of the elbow flexor and extensor muscles and also in different ways activated the distal muscles.

It is possible that the tactile stimuli of various location activate different subsets of the spinal interneurones on their way to appropriate motoneurones. There are several examples of such "private pathways" or "specialized reflexes" elicited by the activation of the cutaneous afferents of the plantar aspect of the foot or the skin area overlying the extensor muscles in the hindlimb (Hagbarth 1952, Engberg 1964, Lundberg 1973). Recently, it was also found that a cutaneous excitation of the flexor digitorum longus motoneurones was controlled in a different way when stimuli were applied either to the dorsal or to the plantar aspect of the paw (Moschovakis et al. 1991). The present results indicate that one can also expect different control of the muscles acting not only at the distal but also at more proximal joints by the tactile stimuli applied either to the dorsal, medial or to the lateral sides of the paw.

THE EFFECTS OF THE TACTILE STIMULI ON THE SOLEUS MOTONEURONES EXCITABILITY: THE H-REFLEX TECHNIQUE IN RATS

To measure the effects exerted by the tactile stimuli applied to various sites of the body the Hoffmann (H) - reflex technique was used in awake chronic animals. The H - reflex (an analog of the monosynaptic stretch reflex) of soleus muscle was elicited by an electrical stimuli applied to the tibial nerve by chronically implanted cuff electrodes. Our preliminary studies showed that tactile stimuli applied to the lateral aspect of the hindpaw led to a clear-cut decrease of the H-reflex size as compared to the control values (Czarkowska-Bauch, Porowska, Przeniosło and Sokołowska, in preparation). These data are in line with our earlier observations on the lateral contact placing reaction in the forelimb (Czarkowska-Bauch et al. 1993, Czarkowska-Bauch 1996 in press). They showed that the tactile stimulation of the lateral side of the forelimb exerted an excitatory effects mainly to the elbow flexor muscles but not to their antagonists. It might be suggested that the tactile stimuli applied to the lateral aspect of the paw and foot exerts similar inhibitory effects on the extensor motoneurones acting at the elbow or at the ankle joint.

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