Activity of the elbow flexor and extensor muscles during contact placing elicited by tactile stimulation of various aspects of the forelimb in the cat

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Abstract. The activity of the biceps brachii and lateral head of the triceps brachii were compared during the contact placing reactions elicited by tactile stimuli applied to the lateral, medial or dorsal aspects of the forepaw to verify the hypothesis that common movement strategy was used in all these reactions. Similar latencies and patterns of muscle activation have been found for the medial and dorsal placing while the different timing of the muscle activation was seen in lateral placing reactions. Both muscles often coactivated during lateral or dorsal and less frequently during medial placing reactions. In dorsal placing the coactivations predominated at the beginning of the reactions while in lateral placing they appeared most frequently in later phases of the reaction. The co-contraction of the elbow flexor and extensor muscles leads to locking of the elbow joint. Thus, the coactivation of these muscles in different phases of the lateral, medial and dorsal placing reactions indicates that various movement strategies have been used as the elbow flexion movement is initiated in different phases of these reactions.

Key words: contact placing, forelimb muscles, forelimb movements, cat
INTRODUCTION

Contact placing (CP) reactions are elicited by light tactile stimuli applied to the distal part of an unsupported limb and result in the placement of this limb on the touched object. It has been assumed that tactile stimulation of various aspects of the paw led to similar reactions which differed only by directional components (Bard 1933; Amassian 1979; Forssberg 1979). In the majority of CP reactions elicited by stimuli applied to the dorsal side of the forepaw (dorsal CP), the elbow flexor and extensor muscles strongly coactivated at the beginning of the reaction (Czarkowska-Bauch and Bem 1988, Czarkowska-Bauch 1990). Co-contraction of these antagonistic muscles locked the elbow which delayed its flexion and allowed movement to start at the proximal and distal joints (Czarkowska-Bauch 1990). A similar strategy of movement has been utilized during perturbation of the early swing phase of locomotion elicited by tactile stimuli applied to the dorsum of the forepaw (Drew and Rossignol 1985, 1987). Perturbation of the swing phase of locomotion by tactile stimuli applied to the dorsum of the hindpaw led also to similar reactions: the ankle joint locked, its flexion was delayed and the reaction started at proximal and distal joints (Wand et al. 1980). All those data indicate that a common element of movement strategy has been involved in all reactions elicited by tactile stimuli applied to dorsal aspects of the paw. The question arises whether the location of the stimuli on lateral or medial aspects of the forepaw influences that strategy of movement.

Our aim was to investigate the pattern of activation of the elbow flexor and extensor muscles during placing reactions elicited by stimulation of lateral and medial aspects of the forepaw and to compare it with those found in dorsal CP reactions. The data revealed that the strategy of movements in CP reactions elicited by stimulation of lateral, medial or dorsal aspects of the forepaw differ substantially as indicated by analysis of coactivation of the elbow flexor and extensor muscle.

METHODS

The experiments were carried out on two adult cats of either sexes. CP reactions were tested when these cats were placed in a specially designed hammock to which they were well accustomed (Czarkowska and Majczyński 1985). All their limbs hung freely and the cats could not see them. To elicit CP reaction the experimenter gently brushed the fur and/or skin over the medial side of the second phalange (medial CP) or over the ulnar side of the fifth phalange (lateral CP), in a proximo-distal direction, with a tactile stimulator. This induced the animal to place the forelimb on the "landing" plate of the apparatus as described before (Czarkowska and Majczyński 1985).

The electromyographic (EMG) activities of the biceps brachii (Bi) and lateral head of the triceps brachii (LaT) muscles were recorded with bipolar, stainless steel EMG electrodes which were chronically implanted as described by Loeb (1979) (see also Czarkowska-Bauch and Bem 1988). The exposed tips of the Teflon- insulated, stranded wires (Bergen Wire Rope, BWR 3.48) were buried into the middle of the muscle belly with a thin, curved, sewing needle and tied over the muscle. The wires were drawn subcutaneously and connected to a multipin contact attached to the skull. The electrodes were implanted under sodium pentobarbital (Nembutal) anesthesia (35 mg/kg i.p.) with Fenactil premedication (1 mg/kg i.m. given 1/2 h before Nembutal).

The EMG activity was recorded with a differential preamplifier (low frequency filter 50 Hz and high frequency filter 2,000 Hz) and stored on the tape of a 7 channel tape recorder (Racal, Great Britain). For further analyses the stored signals were printed using an EMG recorder (Mingograph, Elema-Siemens) with the time resolution of 10 ms/mm. In the case of fragmented activity, the latencies of the earliest bursts and the times of onset of the later bursts, as well as the duration of all bursts were calculated. A group of at least three "spikes" was classified as a burst if it was separated from the next event by 15 ms or more (Fig. 1B in
Czarkowska-Bauch and Bem 1988). For each analysed response, the duration of stimulation and the reaction time (i.e., the interval between the onset of the tactile stimulation and the time of contact of the paw with the "landing" plate of the apparatus) were measured. For some kinds of analyses the data were normalized; the times of onset and the duration of bursts were then expressed as a percent of the reaction times.

RESULTS

Both lateral and medial CP reactions were elicited regularly, appearing in over 90% of the trials. The reaction times were similar to those previously reported (Czarkowska and Majczyński 1985). The median reaction times of lateral CP were 356 and 475 ms in cats A and B, respectively. They were significantly shorter than in medial CP reactions which were 441 ms in cat A and 538 ms in cat B.

The EMG activity of the elbow flexor and extensor was fragmented with variable number of bursts both during medial and lateral CP reactions. Figure 1 shows differences between the elbow flexor activity during lateral and medial CP reactions. Bi was activated during one distinct period of the reaction during medial CP and in a diffused way during lateral CP (Fig. 1).

Medial contact placing reactions

THE ELBOW FLEXOR ACTIVITY

Bi responded with very short latencies to stimulation of the medial side of the paw (Table I). Its activity occupied the first 60% of the reaction time (Fig. 1). Figure 2 shows that distributions of the times of onset of the first two bursts (I, II) of Bi activity were unimodal and the narrow peak of the first burst indicates small variability. In the majority of the reactions the times of onset of the first two bursts coincided with the initial 5% (I), and 10-30% (II) of the reaction times (Fig. 2). The duration of Bi activity was 121 ms in cat A and 169 ms in cat B (median values) which corresponded to 25% and 40% of the reaction times, respectively.

Fig. 1. Patterns of activation of the biceps brachii (Bi) and lateral head of the triceps brachii (LaT) during ten medial (M) and lateral (L) contact placing reactions. Each bar indicates the onset and the duration of EMG activity of the respective muscle during one reaction, expressed as a percentage of the reaction time (RT). Dots indicate normalized stimulation times. The arrows indicate that muscle activity lasted more than 50 ms after the limb has been placed on the apparatus.
TABLE I

Activity of the elbow flexor (Bi) and extensor (LaT) muscles during contact placing (CP) reactions elicited by tactile stimulation of the medial (M) or lateral (L) side of the paw. The total duration of muscle activity, the onset and duration of the first burst - median values in cats A and B. Significant ($P<0.01$ or $P<0.001$) differences in the Smirnov-Kolmogorov test between the medial and lateral CP reactions are indicated by one or two asterisks, respectively. Abbreviations: $n$, number of elicited reactions; other explanations as in Fig. 1

<table>
<thead>
<tr>
<th>Muscle</th>
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<th>$n$</th>
<th>Total duration</th>
<th>First burst (I)</th>
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<td>M</td>
<td>L</td>
<td>% of RT</td>
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<tr>
<td>Bi</td>
<td>A</td>
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<td>93</td>
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<td>B</td>
<td>258</td>
<td>256</td>
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<tr>
<td>LaT</td>
<td>A</td>
<td>58</td>
<td>79</td>
<td>19  NS</td>
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<td></td>
<td>B</td>
<td>261</td>
<td>292</td>
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The responses of Bi to stimulation of the medial side of the paw were similar to those during dorsal CP reactions which have been reported earlier (Czarkowska-Bauch and Bem 1988). Both the latencies and the durations of Bi activities were similar in these two reactions. Also, the distributions of the times of onset of the first two bursts of Bi activity during both reactions were similar (Czarkowska-Bauch and Bem 1988).

**THE ELBOW EXTENSOR ACTIVITY**

LaT was activated with highly variable latencies but generally it was most active during the last 50% of the reaction times (Fig. 1). The distributions of the latencies of its activation were multimodal (Fig. 2). The short latency and short-lasting responses, which appeared only in about 30% of CP reactions, were within the same range as for the elbow flexor and they coincided with the first 10% of the CP reaction times (Fig. 2). In about 30% of the reactions, LaT activation appeared with latencies between 200 and 300 ms which usually corresponded to the last 40% of the reaction times (Fig. 2). In the remaining reactions the muscle was activated with variable latencies (Fig. 2). The times of onset of later bursts were also highly variable (Fig. 2). The total duration of LaT activity was 98 ms in cat A and 141 ms in cat B (median values) which corresponded to 19% and 27% of the reaction times, respectively.

Responses of LaT to stimulation of medial side of the paw were more variable than those observed during stimulation of the dorsal aspect. The short-latency responses appeared less frequently during medial than dorsal CP reactions (Czarkowska-Bauch and Bem 1988). Generally, LaT was less active during medial than dorsal CP reactions and the total duration of its activation was, on average, shorter by about 8% of the reaction times when medial side of the paw was stimulated.

**Lateral contact placing reactions**

**THE ELBOW FLEXOR ACTIVITY**

Bi responded to stimulation of the lateral side of the paw with significantly longer latencies than to stimulation of the medial aspect (Table I). Its activity was scattered throughout the reaction times (Fig. 1). Figure 2 shows broad peaks of distributions of the time of onset of the first three bursts (I-III) of Bi activity which also indicate greater variability than that observed during medial CP reactions. The duration of Bi activity was 194 ms in cat A and 160 ms in cat B (median values) which corresponded to 56% and 37% of the reaction times, respectively (Table I). The duration of Bi activity in the lateral CP was longer by about 14% of the reaction times than to stimulation of medial side ($P<0.0001$).
Forelimb muscle activity during contact placing

The distributions of the onsets of the first three (I to III) bursts of the activity of the biceps brachii (Bi) and the lateral head of the triceps brachii (LaT) muscles during medial (M) and lateral (L) contact placing reactions in cats A (thin line) and B (thick line). The data are expressed in percents of the reaction times.

**THE ELBOW EXTENSOR ACTIVITY**

LaT was activated with variable latencies (Figs. 1 and 2). Its activity occupied mainly the last 50% of the reaction times (Fig. 1). Figure 2 shows that distributions of the times of onset of the first two bursts (I, II) of LaT activity were broad and flat, indicating great variability. The duration of LaT was 65 ms in cat A and 185 ms in cat B which corresponded to 19% and 42% of the reaction times, respectively (Table I).

**RELATIONS BETWEEN THE ELBOW FLEXOR AND EXTENSOR ACTIVITY**

Activity of the elbow flexor usually preceded the activation of the elbow extensor muscle during medial CP and in a majority of the reactions both muscles were activated alternately (Fig. 1). In a small fraction of reactions LaT was activated with latencies similar to Bi and both muscles were coactivated (Figs. 2 and 3). Coactivation of these antagonistic muscles also occurred occasionally in other phases.
of the reaction, but it usually appeared in less than 10% of the reactions (Fig. 3).

Also during lateral CP the elbow flexor activity usually preceded that of the elbow extensor (Fig. 1). However, in contrast to medial CP, a stimulation of the lateral side of the paw frequently produced coactivation of the antagonistic muscles which appeared most often within the initial 25-50% of the reaction times (Fig. 3). Frequent coactivation of Bi and LaT during lateral CP was related to longer latencies and longer duration of Bi activation in the lateral than in the medial CP. It enabled Bi to coactivate not only with short- but also with long-latency responses of LaT.

**DISCUSSION**

The patterns of activation of the elbow flexor and extensor muscles during lateral, medial and dorsal CP reactions indicate that similarities between these reactions are rather superficial. All of these reactions consist of two substantial phases: (1) withdrawal of the paw and (2) placing of the limb on a touching object, but the results indicate that quite different strategies of movement have been used in these reactions. Stimulation of the lateral side of the forelimb led to longer latency and longer lasting activation of the elbow flexor muscle than stimulation of the medial or dorsal aspect of the paw. Also, the pattern and the timing of activation of the elbow extensor muscle were different during lateral than during medial and dorsal CP reactions. On the other hand, the timing and pattern of activation of Bi during medial and dorsal CP reactions were similar but those of LaT were different (Czarkowska-Bauch and Bem 1988).

During dorsal CP reactions co-contraction of the elbow flexor and extensor muscles clearly predominated at the beginning of the reaction (Czarkowska-Bauch and Bem 1988, Czarkowska-Bauch 1990). It was suggested that the early co-contraction was responsible for locking the elbow joint at the beginning of the reaction. Neither during medial nor lateral CP reactions did co-contraction of the elbow flexor and extensor muscles predominate at the beginning of the reaction. During medial CP reactions
both muscles coactivated seldom whereas during lateral CP reactions coactivation occurred very often but in later phases of the reaction. Thus, our results indicate that strategy of the movement with delayed elbow flexion and the reaction initiated at the proximal and distal joints was typical for the dorsal but not for the medial or lateral CP reactions.

Our results indicate that tactile stimulation of the medial or lateral sides of the paw not only add excitation of the adductor in the medial CP and of the abductor in lateral CP to basic flexion-extension movement, as was suggested by Forssberg (1979), but it totally changes the movement strategy due to different timing and the pattern of activation of the elbow flexor and extensor muscles in these reactions.

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REFERENCES


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