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Chapter III

Patterns of hindlimb muscle use and distribution of activity within peroneus longus of the cat.

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PATTERNS OF HINDLIMB MUSCLE USE AND DISTRIBUTION OF ACTIVITY WITHIN PERONEUS LONGUS OF THE CAT

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Summary
In freely moving cats, implanted electromyographic (EMG) electrodes were used for simultaneously recording the activity of the hindlimb muscle peroneus longus (PL) and several of its potential agonists and antagonists (extensor digitorum longus, ED; gastrocnemius lateralis, LG; soleus, SO; tibialis anterior, TA; tibialis posterior, TP). The PL activity was recorded from anterior (PLa) and posterior (PLp) muscle portions, and changes in the PLa/PLp ratio were analyzed in relation to the activity of the other sampled muscles. Large PLa/PLp changes were frequently taking place. A small PLa/PLp ratio (i.e. PLp > PLa) occurred relatively often in motor "events" during which potential PL antagonists were active or potential PL agonists were silent. For small PLa/PLp ratios (i.e. PLa > PLp) the opposite conditions were more favourable. It is concluded that, in spontaneous motor behaviour, the antero-posterior distribution of PL activity is related to basic aspects of the spatial co-ordination of different hindlimb muscles.

Introduction
In studies of the activity of skeletal muscles during motor behaviour each single muscle is often regarded as a physiological unit and the analysis of muscle co-ordination then becomes a matter of studying which combinations of muscles are used together and in which proportions (e.g. Engberg and Lundberg, 1969; Abraham and Loeb, 1985). However, several observations have indicated that different portions of the same muscle may be preferentially activated in different "tasks" (cf. "task group" concept of Loeb) (Loeb and Gans, 1986). One of the most clearly described examples comes from the human biceps brachii (long head) in which units active only in flexion were located mostly laterally and those active only in supination were all located medially (ter Haar Romeny et al., 1984). Furthermore, the same authors also noted that these differences were not in any obvious manner related to the mechanical actions of the units: no differences were found between lateral and medial portions of biceps brachii with regard to torques in supination vs. flexion direction.

We have previously been studying heterogeneous patterns of muscle activation in the cat's peroneus longus muscle (PL). In anaesthetized animals the antero-
posterior distribution of electromyographic (EMG) activity was dependent on how the PL motoneurone pool was activated (peripheral reflex vs. cortical stimulation) (Kandou and Kernell, 1989). In freely moving cats, the posterior PL portions were preferentially activated when standing on the hind-feet or taking off for a jump and anterior PL portions were favoured when preparing to land (Hensbergen and Kernell, 1992). In many other fragments of motor behaviour, anterior and posterior PL portions seemed to be used together in a more balanced manner.

For the cat's PL muscle, a rough correlation exists between the rostro-caudal position of PL motoneurones in the spinal cord and the antero-posterior sites of their motor units in the muscle: cranial motoneurones preferentially innervate anterior PL portions and vice versa (Donselaar et al., 1985). The anteroposterior differences in PL muscle activation during normal motor behaviour suggest that rostral and caudal PL motoneurones have different connectivities within the spinal cord, thus becoming preferentially engaged in different "motor fragments" ("motor primitives"). However, it is not self-evident that motor fragments with an anterior vs. posterior PL preference also differ consistently in their patterns of muscle combinations. The present analysis was undertaken because we wanted to find out whether, during spontaneous motor behaviour, there is a simple and consistent relation between the antero-posterior distribution of PL activation and the spatial pattern of muscle activation within the same hindlimb.

**Methods**

The experiments were performed on five adult, female cats (cats F, L, M, S and V; weights 2.6 - 4.8 kg; ages 4-6 years), including the same animals as those also used by Hensbergen and Kernell (1997). They were provided with chronically implanted EMG recording electrodes in one of their hindlegs (3 cats rightside, 1 cat leftside, 1 cats first leftside and during a second operation rightside). The animals were permitted to move in a largely unrestrained fashion while EMG activity was monitored from anterior (PLa) and posterior (PLp) portions of the peroneus longus muscle. Simultaneously, recordings were also obtained from several of the following neighbouring muscles: soleus, SO; extensor digitorum longus, ED; tibialis posterior, TP; gastrocnemius lateralis, LGa anterior side, LGp posterior side; tibialis anterior, TAA anterior side, TAp posterior side. EMG and video recordings of the motor behaviour of the cats were stored on tape. General qualitative features of the EMG reactions were similar in all the five cats; this similarity included, for instance, the common occurrence of antero-posterior shifts in the PL activity during spontaneous motor behaviour. The detailed analysis of the EMG was restricted to the three most extensively studied animals: cats M, S and V. Further details of the techniques are given below.
Construction and implantation of recording electrodes.
The chronic EMG-electrodes were implanted during an operation performed under general anaesthesia (pentobarbitone, 40 mg/kg i.p.) and aseptic conditions. Two types of electrodes were used: (a) "Patch-electrodes" for the relatively coarse monitoring of whole-muscle activity (SO, LG, EDL, TA); (b) "Fine-wire electrodes" for more localized recordings from separate muscle regions (PLa, PLp) or small muscles (TP).

The patch-electrodes were similar to those of Loeb and Gans (1986; p.119). A pair of teflon-insulated steel wires were backed by an insulating sheet of silicon rubber; each wire consisted of 7 strands of 0.05 mm each. The interelectrode distance and the length of bared metal per electrode were both about 2 mm. The insulating silicon sheet extended at least 4 mm beyond each bared electrode.

The bipolar fine-wire electrodes consisted of two teflon coated single-stranded stainless steel wires (wire diameter 0.05 mm, Clark Electromedical Instruments, SS-3T). At an intermediate site, the teflon coating was removed from 3 mm of each wire. With a hypodermic needle, the two wires were inserted into the muscle in such a way that the bared recording sites were <1 mm deep (interelectrode distance also <1 mm) and the wire terminations re-emerged at the surface at about 3mm from the bared recording area. The ends of the two wires were then tied together, insulated with silicone paste, and sutured to the muscle surface.

Connecting leads from the patch and fine-wire electrodes were brought under the skin to an incision at the back of the cat and soldered to a connector; between muscle and connector, the single-stranded leads of the fine-wire electrodes were protected by polyethylene tubing (Clay Adams). A silicone sheet was placed between connector and skin, and the connector was anchored to the back with two stainless steel wires looped through holes in spinous processes L2 and L5 (cf. Hoffer et al., 1987).

In connection with electrode implantation, preventive treatment with an antibiotic (amoxycillin, 100 mg per day) was given during seven days, starting one day before operation. After a recovery period of about 8 days, normal gait had returned and EMG observations were started.

After the operation, the position of the electrodes was verified in X-ray photographs. After recovery of the animal, it was repeatedly checked that the various implanted electrodes recorded signals independently from each other during voluntary motor behaviour (i.e. no evident cross-talk).

Recording procedures
During recording sessions, a small 8-channel preamplifier was attached to the back-connector of the cat. The output from this preamplifier was transmitted to the rest of the electronic equipment via a long and flexible cable hanging down
from the ceiling in such a way that the cat could move about freely. The preamplified signals were filtered (bandpass 50Hz - 3kHz), further amplified, and stored on tape (bandwidth DC - 2.5 kHz).

During the recording sessions, the cats were encouraged to engage in many different kinds of motor behaviour. Locomotion was performed forwards and backwards, in a straight line or while turning, on flat or inclining surfaces, up or down stairs. Interesting observations were made while the cat was jumping across a small box or up onto or down from a chair (see Hensbergen and Kernell, 1992). Recordings were also obtained during various kinds of prolonged postures (quiet standing on four or two legs; sitting; lying; etc.) and during paw shaking (elicited by attaching piece of sticky tape to the foot pad) and spontaneous grooming behaviour. Finally, a great variety of EMG patterns could often be observed while the cat was spontaneously playing around with small objects on the floor (e.g. playing with a toy mouse or a piece of rope; manipulating and playing with a piece of meat obtained as a reward).

EMG was generally recorded with amplifications set such that PLa and PLp were of similar amplitude during standard straight-forward locomotion. This setting facilitated the discovery of changes in the PLa vs. PLp ratio.

Data analysis
The total amount of recorded EMG exceeded 10 hours. Out of this material, 105 continuous pieces of about 25 s each were selected for the further detailed analysis ("selection-strips"). The following criteria were used for this selection:
-- 1/ High quality recordings (no artefacts) had to be present for PLa, PLp and at least 2 other muscles.
-- 2/ Pieces were favoured that included interesting "EMG-events", particularly those showing variations in the PLa vs. PLp relation (cf. Hensbergen and Kernell, 1992). Although the ultimate selection included all types of PLa vs. PLp ratio (PLa > PLp, PLa ≈ PLp, PLa < PLp), it should be stressed that cases of unbalanced PL activity might well be over-represented in our material. Our main object was not to study how often such unbalanced activity occurs but rather to analyze the conditions (e.g. muscle synergies) associated with its appearance.

Table 1 gives an overview of the various selection-strips and the muscle combinations available within them. The further analysis of the selection-strips was mainly done using good-quality print-outs of the EMG signals, made with a high-frequency chart-recorder (DC-2.5 kHz, Gould TA2000). Complementary information was obtained from the original tapes (EMG- and video-recording) and, to some extent, from digitized versions of the taped selection-strips.

We analyzed the muscle synergies and their possible relation with different PLa/PLp ratios using two alternative techniques:
-- 1/ The "continuous approach", relating the measured and continuously gradable amounts of neighbouring muscle activity to the PLa/PLp ratio. In this
approach, digitized selection-strips were used, and as many as possible of apparently separate EMG bursts of PL were identified by eye and marked, using commercially available software (Data-Pac II). Between 18-66 such bursts (average 38) were marked in each selection-strip. EMGs were rectified and smoothed (time constant 25 ms) and average amplitudes were calculated within each burst. For PL, the antero-posterior ratio of the EMG-amplitudes was also calculated and compared to the similarly measured relative EMG-amplitudes for other neighbouring muscles. This analysis was made using 346 events from 3 different cats (3 pooled selection-strips from one recording session for each cat).

-- 2/ The "on/off approach", relating the PLa/PLp ratio to the (apparent) absence or presence of activity in various neighbouring muscles. Also in this case, PL-"events" were identified by eye within each one of the selection-strips. However, in this case the PL activity of each event was only categorized into one of three groups: PLa>PLp, PLa<PLp or PLa~PLp. A required condition for this analysis was that EMG amplification was indeed set such that, in simple locomotion, the PLa and PLp activities were displayed at about the same size. The activity of neighbouring muscles was simply classified as to whether each recorded individual muscle was active or silent during the event. In these cases, events were critically selected that could be clearly classified (by eye) according to these simple principles and which, in addition, included a sufficiently great number of unbalanced PL activity (i.e. PLa>PLp or PLa<PLp). On average, only about 3 on/off events were selected in each selection-strip; the total material included 307 events from 105 strips.

For the statistical analysis of the results, use was made of standard versions of t tests, chi-square tests, and calculations of linear correlation coefficients.

Results

Figure 1 shows a sample from our EMG recordings, illustrating changes in the PLa/PLp-ratio during ongoing motor behaviour (see Legend). Three time-segments are labelled a, b and c. In segment a and c, the activity of PLa clearly exceeds that of PLp. In segment b, the opposite relationship is seen. In an earlier publication, at least some of such changes were found to be associated with recognizable fragments of motor behaviour (e.g. jumping and landing, Hensbergen and Kernell, 1992). In the present context we investigated whether changes in the PLa/PLp ratio were associated with recognizable patterns of muscle synergy.

Continuous approach

In all analysis strips, the PLa/PLp ratio was found to vary over a wide range (Fig.2 B, D). Peaks of the PLa/PLp ratio were higher for weak PL activation than for higher activity levels and the relation between PL activity and the PLa/PLp ratio typically showed a negative correlation; such correlations were most clearly
Table 1.

<table>
<thead>
<tr>
<th>Number of strips</th>
<th>Available muscle EMGs</th>
<th>Number of on/off events</th>
<th>Cat</th>
</tr>
</thead>
<tbody>
<tr>
<td>7</td>
<td>PLa, PLp, SO, ED</td>
<td>11</td>
<td>V</td>
</tr>
<tr>
<td>38</td>
<td>PLa, PLp, SO, ED, TP</td>
<td>95</td>
<td>V, S</td>
</tr>
<tr>
<td>31</td>
<td>PLa, PLp, SO, ED, Tap</td>
<td>101</td>
<td>M</td>
</tr>
<tr>
<td>13</td>
<td>PLa, PLp, SO, ED, TAp, LGa, LGp</td>
<td>62</td>
<td>M</td>
</tr>
<tr>
<td>16</td>
<td>PLa, PLp, SO, TAa, TAp, LGa, LGp</td>
<td>38</td>
<td>M</td>
</tr>
<tr>
<td>Total: 105</td>
<td></td>
<td>Total: 307</td>
<td></td>
</tr>
</tbody>
</table>

Abbreviations: PL peroneus longus; SO soleus; ED extensor digitorum longus; TP tibialis posterior; TA tibialis anterior; LG gastrocnemius lateralis; a anterior; p posterior

present for the posterior PL muscle activity (Table 2; cf. Fig.2 B, D). Thus, although low PLa/PLp ratios might be found at almost any level of activity, the chance of finding a very high ratio was generally greater at weak levels of muscle activation. The variation in PLa/PLp ratio did not mean, of course, that the two portions of PL acted independently of each other: in all cats a marked and significant positive correlation was found between the PLa and the PLp activity (Fig.2 A, C).

As is illustrated by the results shown in Fig.3, no clear and consistent relationships were found between the PLa/PLp ratio and the activity level of other muscles than PL itself. The correlation in Fig.3A was significant but exceedingly weak ($r^2 = 0.046$) and a significant correlation was found in only one other instance out of 11 analyzed data sets (Table 2).

An analysis of the general relationships between the activity of the different hindlimb muscles falls outside the scope of the present context. However, it is of interest to note that we hardly ever found any significant correlation between the activity level of PLa or PLp and that of its most direct antagonists SO or TP ($P>0.05$ for 9 out of 10 data sets; $r^2 = 0.08$ for one case of TP vs. PLp). In contrast, significant correlations were in all measured cases found between the activity of SO vs. LG (positive), SO vs. TP (positive) or SO vs. TA (negative). The level of ED activity commonly showed a weak but significant positive correlation with PL ($P<0.05$ for 3 of 4 data sets).

On/off approach.
Among the co-ordination patterns (combinations of active muscles) studied in the present analysis, almost none were consistently associated with a given category of PLa/PLp unbalance (e.g. 100% PLa<PLp or PLa>PLp; Figs.4-5). However, the probability of getting a given type of PLa/PLp relation was clearly related to
whether the particular neighbouring muscles were active or silent. This is demonstrated by the two graphs of Fig.4, in which the relative frequency (%) of the three categories of PLa/PLp relation has been plotted versus the presence of activity (A) or silence (B) in other, simultaneously sampled muscles. In both graphs there is a continuous shift in the probability for a given PLa/PLp-category depending on which other muscle is either active (A) or silent (B). Furthermore, the findings of Fig.4 are characteristic in demonstrating that the two categories PLa>PLp and PLa≈PLp behaved in a very similar manner, both being reciprocal to the behaviour of the category PLp>PLa in their relation to other muscle activity.

The chi-square calculations of Table 3 demonstrate that differences such as those illustrated in Fig.4 were statistically highly significant. The relative chance of favouring the posterior portion of PL (PLp>PLa) was significantly greater with than without simultaneously ongoing activity in potential PL antagonists, i.e. the post-tibial extensor soleus or the foot-inverter tibialis posterior. Conversely, the
Fig. 2. "Continuous analysis". Plot of measured amount of EMG activity (arbitrary units) of PLa vs. PLp (A, C) and of the PLa/PLp ratio vs. the level of PLp activity (B, D), as plotted separately for cats V (A, B; n = 193) and M (C, D; n = 81). In the few cases of a PLa/PLp ratio exceeding 10 it was set to a value of 10 in the plot. All sampled "continuous" events included for each cat. Correlation coefficients (all P < 0.001): A = 0.86; B = -0.50; C = 0.83; D = -0.46. Amount of rectified and smoothed EMG activity measured as average value per event.
Fig. 3. "Continuous analysis". Plots of measured activity levels of ED (A) and SO (B) vs. the PLa/PLp ratio. Data for all the 193 sampled "continuous" events of cat V. For statistics, see Table 2.

Table 2.

<table>
<thead>
<tr>
<th>Muscle activity</th>
<th>Cat-M</th>
<th>Cat-S</th>
<th>Cat-V</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>81 events</td>
<td>72 events</td>
<td>193 events</td>
</tr>
<tr>
<td>Correlation vs. PLa/PLp ratio</td>
<td>+0.48</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>ED</td>
<td>ns, ns</td>
<td>ns, ns</td>
<td>ns, ns</td>
</tr>
<tr>
<td>LGa, LGp</td>
<td>ns, ns</td>
<td>ns, ns</td>
<td>ns, ns</td>
</tr>
<tr>
<td>SO</td>
<td>ns, ns</td>
<td>ns, ns</td>
<td>ns, ns</td>
</tr>
<tr>
<td>TAa, TAp</td>
<td>ns, ns</td>
<td>ns, ns</td>
<td>ns, ns</td>
</tr>
<tr>
<td>TP</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PLa, PLp</td>
<td>ns, -0.46</td>
<td>ns, -0.54</td>
<td>-0.39, -0.50</td>
</tr>
</tbody>
</table>

All noted correlation coefficients were statistically significant (P < 0.05).
Abbreviation: ns, not significant (i.e. P > 0.05).

dorsiflexors: extensor digitorum longus, tibialis anterior).
We also analyzed the relation between the occurrence of a given category of PLa/PLp unbalance and combinations of activity/inactivity in other sampled
Fig. 4. "On/off analysis". Relative frequency of occurrence of different PLa/PLp categories as seen during the simultaneous presence (XX+: panel A) or absence (XX-: panel B) of activity in other muscles. See Table 1 for muscle abbreviations. All the 307 sampled on/off events from all cats combined. For each plotted category along the x-axis, the number of events classified as PLa > PLp, PLa = PLp and PLa < PLp were counted (cf. some of the raw data in Table 3). The plot shows these counts as normalized (%) in relation to the total number of cases within each plotted x-axis category (n=15 or higher). Cases ordered in relation to the relative frequency of PLp > PLa. Plot-symbols: see Legend.

Figures show the percentage of on/off events categorized as PLa > PLp, PLa = PLp, and PLa < PLp for different muscles. Panel A shows the results for muscles active, while Panel B illustrates the results for inactive muscles. The x-axis represents different muscles, and the y-axis shows the percentage of events categorized. The plots are ordered according to the relative frequency of PLp > PLa.

Discussion
Our results confirmed that, during spontaneous motor behaviour, there are large variations in the antero-posterior distribution of EMG-recorded PL activity (Figs.1-3). Our quantitative EMG analysis failed to show any clear relationship between these antero-posterior differences and the activity level of other individual PL-agonists or -antagonists (Fig.3, Table 2). In contrast, our largely qualitative "on/off" analysis, using data from a greater number of selection-strips, did show evidence for a relationship between antero-posterior PL patterns and the presence or absence of activity in other muscles (Fig.4, Table 3): activity in potential agonists and silence in potential antagonists favoured anterior PL muscles. These results are summarized in Fig.5 for combinations of two (A-B) or three (C-D) other muscles. Essentially, the results seemed similar to those for the single-muscle analysis (Fig.4): in both cases the probability for encountering a given type of PLa/PLp unbalance shows a gradual shift from one muscle combination to another. However, also here there seemed to be no drastic step-wise change in PLa/PLp behaviour from one co-ordination pattern to the next.
portions, and vice versa. These findings fit well to our earlier observations concerning the relationships between motor behaviour and antero-posterior PL ratios: posterior PL activity was particularly favoured when standing on the hindlegs or taking off for a jump, i.e. when activating post-tibial extensors (cf. Fig.4).

At first sight it seems paradoxical that our "on/off" analysis gave significant results (PLa/PLp relation vs. presence or absence of other muscle activity, Fig.4, Table 3) while our "continuous" analysis failed to do so (PLa/PLp ratio vs. amount of other muscle activity, Fig.3, Table 2). However, it should be realized that these two kinds of measurement are not equivalent: the "on/off" approach merely concerns the presence or absence of co-activation between two muscles;

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Fig. 5. "On/off analysis". Plot like that of Fig.4, showing the relative frequency of different PLa/PLp categories vs. the activity or silence of simultaneously sampled muscles. In panels A-B the comparisons concern pairs of simultaneously sampled muscles and in panels C-D triples (as far as available in sufficient numbers, i.e. \( n \geq 8 \)). Panels A and C from cat M; panels B and D from cats V and S.
once both muscles are active, the relationship between their respective levels of activity might be highly variable.

It is still unclear what the functional meaning might be of a preferentially anterior or posterior PL activity. In most tasks slow-twitch motor units seem to be those preferentially activated at weak forces (Henneman and Mendell, 1981); in some particular tasks the opposite appears to be the case (e.g. Nardone et al., 1989; Smith et al., 1980). However, for the cat's PL muscle, such shifts in the preferential recruitment of different contractile types of units would not be expected to be associated with antero-posterior shift in the EMG activity. Rostral

Table 3.

<table>
<thead>
<tr>
<th>Muscle activity</th>
<th>PLa&lt;PLp</th>
<th>Pla&gt;=PLp</th>
<th>P (chi-square)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>%</td>
<td>n</td>
</tr>
<tr>
<td>ED+</td>
<td>106</td>
<td>45.1</td>
<td>129</td>
</tr>
<tr>
<td>ED-</td>
<td>31</td>
<td>91.2</td>
<td>3</td>
</tr>
<tr>
<td>TAp+</td>
<td>75</td>
<td>55.6</td>
<td>60</td>
</tr>
<tr>
<td>TAp-</td>
<td>46</td>
<td>74.2</td>
<td>16</td>
</tr>
<tr>
<td>TP+</td>
<td>21</td>
<td>46.7</td>
<td>24</td>
</tr>
<tr>
<td>TP-</td>
<td>1</td>
<td>2.0</td>
<td>49</td>
</tr>
<tr>
<td>GLp+</td>
<td>15</td>
<td>100</td>
<td>0</td>
</tr>
<tr>
<td>GLp-</td>
<td>41</td>
<td>53.9</td>
<td>35</td>
</tr>
<tr>
<td>SO+</td>
<td>84</td>
<td>75.0</td>
<td>28</td>
</tr>
<tr>
<td>SO-</td>
<td>62</td>
<td>32.5</td>
<td>129</td>
</tr>
</tbody>
</table>

Statistical analysis (chi-square) of data used for Fig. 4 A-B. Second and third columns give number of "on/off" events showing the indicated kind of antero-posterior PL activity.
and caudal PL motoneurones (preferentially innervating anterior and posterior PL portions) are widely overlapping with regard to the contractile properties of their motor units (Kernell et al., 1985). Furthermore, anterior and posterior PL portions have the same muscle fibre composition with regard to type I vs. II fibres (i.e. "slow" vs. "fast" fibres; Kernell et al., 1998). Considering the PL anatomy, a slender muscle with a long and narrow distal tendon, it also seems unlikely (but still has to be proven experimentally) that anterior and posterior PL units would produce ankle torques of significantly different directions. Possibly, the antero-posterior differences in PL activation reflect differences in the central connectivity to rostral and caudal PL motoneurones which are motivated by central (developmental?) rather than by peripheral conditions (cf. Kernell, 1992).

The present investigations merely represent a first step towards an increased understanding of how different portions of the PL muscle, and of the PL motoneurone pool, are connected into different spatial patterns of coordination, i.e. into different "motor primitives". We think that a further analysis of such questions may be a useful approach when trying to understand the composition and nature of such basic components of motor behaviour and the underlying neuroanatomical connectivity.

**Note.** The recordings analyzed in this article were obtained while the authors were associated with the Department of Neurophysiology at the University of Amsterdam, The Netherlands.

**Acknowledgement.** We would wish to thank dr.O.Eerbeek for his help with operative procedures for the implantation of EMG electrodes.

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