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CURVE WALKING IN CRAYFISH

HOLK CRUSE AND MANUEL G. SILVA SAAVEDRA
Faculty of Biology, University of Bielefeld, PO Box 100131, D-33501 Bielefeld, Germany

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Summary

Curve walking of crayfish *Astacus leptodactylus* was investigated by exploiting their optomotor response. The animal walked while spatially fixed on a motor-driven treadmill and turning behaviour was induced by an optical stimulus, a pattern consisting of vertical stripes moving in a horizontal direction. In this open-loop situation, the crayfish maintains the same step frequency for the legs on both sides of the body for low and intermediate turning speeds, but increases the step amplitude of the outer legs 2, 3 and 4 by shifting the posterior extreme position (PEP) of these legs in a posterior direction and reduces the step amplitude of inner leg 5 by shifting the PEP of this leg in an anterior direction. Furthermore, the main movement direction of the legs can change relative to the body. This was observed for outer leg 5 and also, at higher turning speeds, for outer leg 2. As coordinating influences between contra- and ipsilateral legs were found directly to influence only the anterior extreme position of the legs, these results indicate that the mechanisms controlling curve walking may be different from those controlling normal leg coordination.

Key words: locomotion, walking, leg coordination, crayfish, *Astacus leptodactylus*.

Introduction

Control of leg movements in a multilegged animal can be divided into two areas of interest: coordination of the joints of a single leg and coordination of the movements of different legs. The latter has been investigated in detail for insects and Crustacea (Cruse, 1990). Each leg can be considered to be a separate system performing cyclic step movements. The cycles consist of alternating power strokes and return strokes, and each leg system can be considered to be a relaxation oscillator (von Holst, 1943, 1948; Wendler, 1964, 1968; reviewed by Bässler, 1983). The coupling between these oscillators is controlled by a small number of local rules. For the stick insect, four such rules have been described which act between ipsilateral and contralateral legs, whereas in the crayfish only two ipsilateral mechanisms and one contralateral mechanism are known. Two other mechanisms reported for the stick insect (Cruse, 1990) and one for the crayfish (Müller and Clarac, 1990) are likely to be active only during emergency situations, for example, under conditions of high load. In all these investigations, intact animals walking in a straight line have been used. In contrast, curve walking has been studied rarely and less systematically.

Curve walking results when the legs on the outer side of the curve move the body at a somewhat higher velocity than the inner legs. For the stick insect, Graham (1972) and Jander (1985) have shown that step amplitude and, for sharper turns, step frequency of the outer legs increases. For other insect species (honeybee, Zolotov *et al.* 1975; cockroach, Franklin *et al.* 1981; Camhi and Levy, 1988), a similar combination of both strategies has been described. For ants, Zollikofer (1994) found that the stride length of the inner side of the curve is shortened, whereas the stride length of the outer legs remains approximately constant. Strauß and Heisenberg (1990) found similar results for *Drosophila melanogaster*. It should, however, be noted that stride length is measured using absolute coordinates, whereas step amplitude is measured using a body-fixed coordinate system; hence, the two measurements are not directly comparable. J. Dean and A. Rixe (personal communication) note that curve walking can also be produced if, during the stance phase, the leg actively produces a trajectory which deviates from a line parallel to the long axis of the body. This has been found for the honeybee (Zolotov *et al.* 1975) and for the cockroach when escaping from a lateral wind puff (Camhi and Levy, 1988). Such a deviation could be produced by changing the strength of the forces applied in the transverse direction, as found by Full and Tu (1990) for the cockroach. For the crayfish *Astacus leptodactylus*, Müller and Cruse (1991*a*) studied the leg coordination of animals walking on two motor-driven belts operating at slightly different speeds for the right and left legs. In these experiments, the anterior extreme position (AEP) of all legs was found to shift posteriorly. This effect was attributed to a coupling mechanism between contralateral legs. However, it is not clear whether their experimental arrangement corresponded to an animal walking in a straight line but receiving a continuous disturbance stimulus, or whether it corresponded to an animal negotiating active turns. In the experiments reported here, we

therefore applied a stimulus that is known from many earlier studies to elicit active curve walking (e.g. Hassenstein, 1958; Götz and Gambke, 1968; Heisenberg and Wolf, 1988). The crayfish was placed in an aquarium and presented with an optical stimulus consisting of vertical stripes moving in a horizontal direction. The optomotor response to this stimulus consists of active turning movements. In addition, the radius of the curve walked becomes smaller as the speed of the moving stripes increases.

When the animals are spatially fixed (different techniques have been used by different authors to achieve this), an open-loop situation is created in which the reaction of the animal does not compensate for the stimulus. Several authors have shown that an optomotor response can be elicited even when only a small part of the optic field contains a moving stimulus (Hassenstein, 1958; Götz and Gambke, 1968; Götz and Wenking, 1973). In most of these cases, the optomotor response was used to measure the strength of the turning tendency (for example, the radius of the curve walked) but not the detailed movements of the legs. To our knowledge, only Jander (1985) has used this method to investigate leg movements in curve walking by stick insects. Following the same approach, we measured the leg movements of crayfish while they performed active curve walking in an open-loop situation.

Materials and methods

Adult female and male crayfish (*Astacus leptodactylus* Eschscholz), weighing approximately 60 g and obtained from Langbein, Hamburg, Germany, were kept in tanks at a temperature of 12–15 °C. For the experiments, individual animals were fixed dorsally by the carapace to a holder using dental glue and then placed on a motor-driven belt in a water-filled aquarium at the same temperature (Chasserat and Clarac, 1980). The holder was counterbalanced to allow the animal to determine its height above the belt. The animal was fixed to the holder such that only small forward–backward, but no rotational, movements were possible.

In a preliminary experiment, the strength of the coordination between the legs on the right and left sides of the body was investigated in relation to walking (=belt) speed. The results showed that coordination strength increased monotonically between 5 and 10 $cm\,s^{-1}$ (G. Schöner, unpublished data). This is qualitatively in agreement with findings from other species (Cruse, 1990). As the effects of coordination during curve walking were expected to be most obvious when contralateral coupling was weak, we chose a speed of 5 $cm\,s^{-1}$ for all subsequent experiments.

Curve walking was elicited using the classical optomotor response and a similar set-up to that of Götz and Gambke (1968). We arranged three video monitors (Sanyo type 18112CX, screen diagonal 25 cm) beside the aquarium, one in front of the animal and one on each side. The distance between the head of the animal and the screens was 34 cm. The walls of the aquarium were covered with black paper except for the regions containing the monitors. The monitors were connected to a computer (Apple IIe) which was programmed to show vertical green and black stripes (height 14 cm, width 6 cm) moving in a horizontal direction. At the position of the animal, the width of a stripe subtended an angle of approximately 10 °. The speed of the moving stripes was varied between 0.6 and 2.7 $°\,s^{-1}$.

The experimental procedure was as follows. The animal was placed in the aquarium and fixed to the holder above the belt while the monitors were switched off. The belt was then started and run at a constant speed of 5 $cm\,s^{-1}$. After the animal began to walk, as indicated by regular movement of all eight legs while the abdomen was held horizontally with the pereiopods waving regularly, the monitors and moving stripes were switched on. For fast and medium stripe speeds, the animals performed a constant curve-walking behaviour within approximately 10 s of the start of pattern movement. For the slowest stripe speed, this delay increased to 45 s. Therefore, the belt was run at each speed for at least 1 min (up to a maximum of 3 min), and only the last 20–30 s of each experiment were evaluated. For each speed, pattern movement in both directions was tested consecutively. Between each change of the stimulus (speed, direction), the optical stimulus was switched off until normal straight walking was observed for at least 10 s.

The animal was filmed from above using a Panasonic video camera (WV-CD20) at 50 frames s^{-1} and a video recorder (NV-F70). Films were evaluated using frame-by-frame analysis. Geometrical measurements given are normalized to the mean length of the animals and measurement accuracy was ±1 mm. For each walking leg (legs 2–5; the first legs, the chelae, are normally not used for walking), the position of the leg tips at the anterior (AEP) and posterior (PEP) extreme positions during each step were recorded from the monitor. The AEP and PEP values were determined using a body-fixed, two-dimensional coordinate system. The *x*-axis corresponds to the long axis of the body (positive values anterior), the *y*-axis points transversely (positive values to the right). The holder is defined as the origin. As the animals varied in size by a maximum factor of 1.25, the data were normalized to mean body length. For each extreme position, mean values ± S.D. were calculated separately for the *x* and *y* components. Differences between mean values were tested for significance using the *t*-test and the *U*-test. The step amplitude, i.e. the Euclidean distance between the AEP and PEP of a step, was measured directly for each step.

Results

In a preliminary series of experiments, two animals were tested using eight different stripe speeds (0.6, 0.7, 0.8, 1.0, 1.2, 1.5, 2.1 and 2.7 $°\,s^{-1}$). When we used faster stripe speeds, the animals no longer moved the legs on the inner side of the curve. Results from the different stripe speeds were qualitatively grouped into slow (0.6–0.8 $°\,s^{-1}$), intermediate (1.0–1.5 $°\,s^{-1}$) and high (2.1–2.7 $°\,s^{-1}$) speeds, as no obvious differences could be detected within these groups. Fig. 1 gives mean AEP and

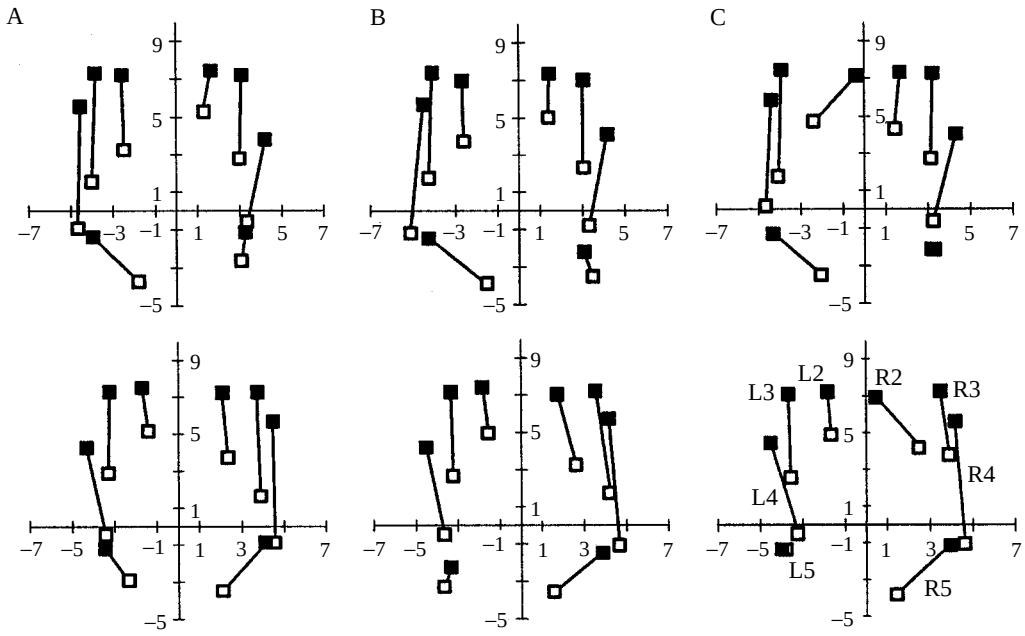

Fig. 1. The anterior extreme position (AEP; filled squares) and the posterior extreme position (PEP; open squares) of the legs with respect to a body-fixed coordinate system (top view). The ordinate represents the long axis of the body, positive values indicate anterior. The abscissa represents the transverse axis. Positive values to the right. Leg positions for three different stripe speeds are given (A) $0.6\,°\,s^{-1}$, (B) $1.2\,°\,s^{-1}$ and (C) $2.7\,°\,s^{-1}$. Mean values for 20 steps, one animal. All measurements are given in cm. Upper figures show right turns, lower figures left turns. AEP and PEP values for one leg are connected by straight lines.

PEP values from one animal for each of these groups for right turns (upper graphs) and left turns (lower graphs). In all experiments, the step frequency, and therefore the step period of the right and left legs, was the same (results not shown). Mean values for step periods of different legs differed by less than 2 % (200 steps for each leg, 10 animals). This shows that curve walking in *Astacus leptodactylus* under these conditions is achieved through changes in the geometrical parameters which determine the movement of the individual legs (i.e. through changes in step amplitude and trajectory orientation, see below) rather than through changes in step frequency.

In order to investigate the effects of these geometrical parameters quantitatively, results for 10 animals were analysed in detail for the three intermediate speeds. Results are presented below for one stripe speed, $1.2\,°\,s^{-1}$, but were similar for all turning velocities investigated. As indicated in Fig. 1, the mean direction of the line connecting the AEP and the PEP changes with turning direction. Therefore, the angle between the lines connecting the mean AEP and PEP values and the vertical (body axis) were determined, and the mean values and S.D. of these angles are shown in Fig. 2A. Significant differences between inner and outer legs were found for legs 2, 4 and 5 ($P<0.001$). The lines connecting the AEP and PEP of a leg are used to measure the mean direction of the leg trajectory. It should, however, be noted that the real trajectories do not follow these straight lines, but are better described by curved lines (not shown). Fig. 2B shows that the step amplitude, i.e. the Euclidean distance between AEP and PEP, also changes during curve walking: the step amplitude on the outer side is significantly larger in all cases ($P<0.001$). The amplitude of the step of leg 5 on the inner side is almost zero for higher stripe speeds (see Fig. 1C). The mean amplitude ratio (outer leg/inner leg) for leg pairs 2, 3 and 4 is 1.24 at $1.2\,°\,s^{-1}$.

To investigate how these changes in amplitude were

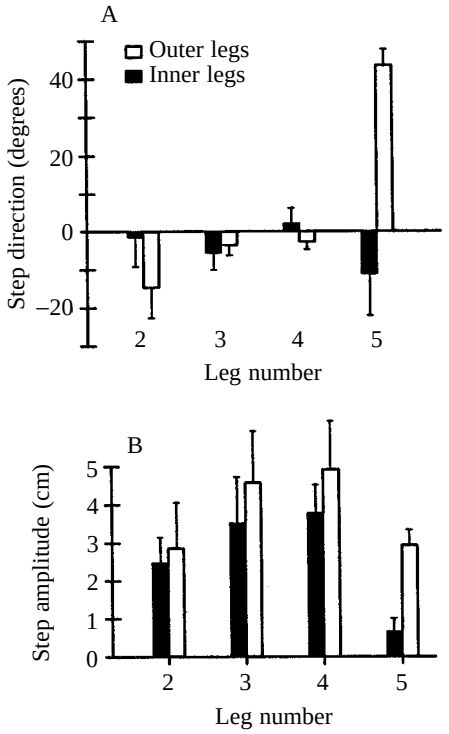

Fig. 2. (A) The direction of the step trajectories. Positive angles indicate that the posterior extreme position (PEP) of the step is nearer to the body than is its anterior extreme position (AEP). Differences for legs 2, 4 and 5 are significant ($P<0.001$). (B) Step amplitude. Comparison of inner (filled bars) and outer legs (open bars). All differences between inner and outer legs are significant ($P<0.001$). Mean + S.D., 10 animals, 20 steps each. All values are for a stripe speed of $1.2\,°\,s^{-1}$.

produced, the differences between mean AEP and PEP values during straight walking and curve walking were determined. The results are shown in Table 1. Significant differences

Table 1. *Differences in the anterior and posterior extreme positions of legs between straight walking and curve walking*

	Inner legs		Outer legs	
	Long (*x*-) axis	Transverse (*y*-) axis	Long (*x*-) axis	Transverse (*y*-) axis
Leg 2				
AEP	–0.14 (>10%)	0.17 (>10%)	0.33 (>5%)	–0.06 (>5%)
PEP	–0.26 (>10%)	–0.13 (>10%)	–0.59 (1.2%)	–0.03 (>10%)
Leg 3				
AEP	0.13 (>10%)	–0.19 (>10%)	0.28 (>5%)	–0.06 (>10%)
PEP	–0.28 (>10%)	–0.08 (>10%)	–1.27 (0.5%)	–0.02 (>10%)
Leg 4				
AEP	–0.20 (>10%)	–0.28 (>10%)	0.29 (>5%)	0.07 (>10%)
PEP	0.23 (>10%)	–0.12 (>10%)	–1.07 (0.8%)	–0.13 (>10%)
Leg 5				
AEP	0.28 (>5%)	0.27 (>10%)	0.30 (4.8%)	0.11 (>10%)
PEP	1.47 (0.8%)	–0.01 (>10%)	–0.32 (>5%)	–1.36 (1.1%)

Values are in cm and are means (10 animals, 20 steps each). Negative values indicate that the position is shifted towards the posterior (long axis) or towards the body (transverse axis) relative to straight walking.

Significance levels (in parentheses) are given in %. Stripe speed is $1.2\,°\,s^{-1}$.

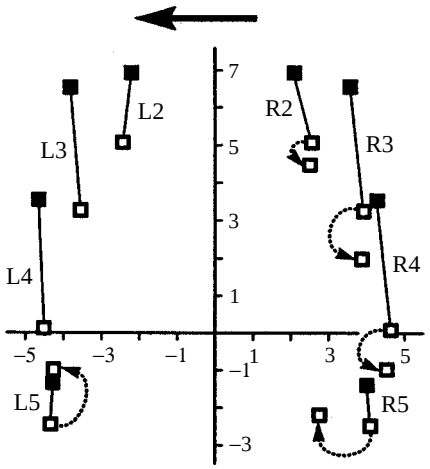

Fig. 3. A summary of the differences between straight walking and curve walking. Anterior extreme position (AEP; filled squares) and posterior extreme position (PEP; open squares). Values are given for straight-walking animals (mean values for 10 animals, 20 steps each). The AEP and PEP of each leg are connected by straight lines. Significant changes found when the animals turn to the left (arrow) are indicated by dashed arrows which point from the straight-walking values to the corresponding values used during curve walking. Stripe speed $1.2\,°\,s^{-1}$. L, left; R, right.

(*t*-test) were found in the PEP of outer legs 2, 3 and 4, which were more posterior during curve walking, and in the PEP of leg 5, which shifted transversely nearer to the body. These changes resulted in an increase in step amplitude of the outer legs. For the inner legs, the only significant effect found was that the PEP of leg 5 moved significantly more anteriorly during curve walking, which decreased the step amplitude of this leg. Similar changes could be detected when curve walking was compared between right and left turns (compare upper and lower graphs of Fig. 1).

The results presented in Table 1 were ambiguous concerning the AEP of outer legs 4 and 5 in that in four animals, a significant anterior shift was found (Fig. 1 shows results from one of these animals), whereas no effect was measured for the other six animals. The data for all animals taken together resulted in a significance level of approximately 5 % for both values.

It was noted qualitatively, but not investigated further, that at higher turning speeds the direction of movement of outer leg 2 became increasingly inclined (see Fig. 1C).

Discussion

In this study, the curve walking of crayfish was investigated using an open-loop situation. As discussed above, several earlier investigations of insects have used this method to elicit curve walking. A motor-driven treadmill was used here to elicit walking, and it has been shown in a number of earlier studies (e.g. Clarac and Cruse, 1982; Cruse and Müller, 1986) that this stimulus is sufficient to elicit walking and that additional transverse optical flow is not necessary. Alternatively, walking can be elicited using transverse optical flow alone (Ayers and Davis, 1977). However, it is not clear whether a behaviour performed under open-loop conditions is qualitatively the same as that performed under closed-loop conditions. According to classical control theory, these situations differ only with respect to the gain; however, recent studies have shown that qualitative differences may occur (Heisenberg and Wolf, 1988; Schöner, 1991). Therefore, further experiments under closed-loop conditions are required to investigate whether our results can also be applied to the closed-loop situation.

For the open-loop situation, our results (summarized in Fig. 3) show that, at least for low and intermediate stripe speeds, the crayfish maintains the same step frequency for the legs on both sides of the body (results not shown), but increases the step amplitude of outer legs 2, 3 and 4 by shifting the PEPs in a posterior direction and reduces the step amplitude of inner leg 5 by shifting the PEP of this leg in an anterior direction. Furthermore, the main direction of movement of the legs may change relative to the body. This is clear for outer leg 5 (Figs 1, 2A, 3) and, for higher turning speeds, also for outer leg 2 (Fig. 1C). Thus, open-loop curve walking is not produced by changing the step frequency of the legs, but by changing the step amplitude and the mean direction of movement of the leg tip. Amplitudes were prolonged by shifting the PEP posteriorly (for outer legs 2, 3 and 4), in a posterior and transverse direction (outer leg 5) or anteriorly (inner leg 5). In some animals, AEP values were also shifted anteriorly, which again increased the step amplitude. As the step frequency of all legs was constant, prolongation of the power stroke must have been compensated by a shortening of the duration of the return stroke. How could the neuronal system controlling leg

movement produce the observed PEP shifts? There might be a change in a centrally produced temporal delay or, alternatively, a shift in the geometrical position that the leg has to reach in order to finish the power stroke. Since the changes in trajectory directions measured in legs 2 and 5 clearly indicate a geometrical effect, the simplest hypothesis is that, as assumed in earlier models of coordination (Cruse and Müller, 1986; Müller and Cruse, 1991*b*), curve walking is achieved by changing the geometrical threshold positions. This assumption might be verified by placing the leg on a platform moving at a different speed from that of the motor-driven belt (Cruse, 1985; Foth and Bässler, 1985).

In contrast to the present results, Müller and Cruse (1991*a*) found a posterior shift of the AEP during straight walking on a split belt with different speeds for the right and left sides. They attributed their findings to a mechanism for coupling of the contralateral legs. This indicates that different mechanisms are involved in the coordination between ipsi- and contralateral legs during straight walking compared with those that control open-loop curve walking. An anterior shift of the AEP was observed during open-loop curve walking in only some animals in the present study. Future research is needed to reveal the nature of cooperation between the mechanisms for coordination between legs during turning and straight walking.

A critical point for consideration in the interpretation of these results is the extent to which the leg movements can be considered to be active movements and the extent to which the results are influenced by passive effects caused by the movement of the treadmill. Return stroke movements are active movements, and therefore the position of the AEP is controlled by the animal. During the power stroke, the legs also move actively. This was shown for lobsters walking on a treadmill by Clarac and Cruse (1982) using force measurements and is also indicated by the oblique mean direction and the curved form of the trajectories in the present study. The latter also shows that the leg tip may slip on the belt surface. The possible influence of the treadmill prevents the drawing of direct conclusions concerning the activity of the motor control system of the animal. This is a fundamental problem, however, which also occurs when investigating animals walking under closed-loop conditions (i.e. untethered). In this case, too, the movement of individual legs results both from the active motor output of the leg itself and also from passive effects, which are, in this case, produced by the other legs moving the body relative to the ground. This problem could be solved by investigating animals walking on a frictionless surface (e.g. Camhi and Nolen, 1981; Cruse and Epstein, 1982), but this situation may create additional problems because a normal force feedback might be necessary to induce natural walking. Interestingly, Camhi and Levy (1988) found no difference between curve walking of the free cockroach and of the cockroach fixed over a frictionless surface. This might, however, be a special property of the escape behaviour considered by these authors. Evidence that in *Drosophila melanogaster* all legs actively contribute to turning is given by Götz and Wenking (1973). In spite of these drawbacks, the results presented here show that, under open-loop conditions, curve walking influences the positioning of the end of the power stroke (the PEP), whether this is due to a purely geometrical effect or combined with temporal influences.

Zollikofer (1994) reports that ants maintain the stride length of the outer legs and decrease the stride length of the inner legs during curve walking. Stride length was measured in absolute coordinates and not using a body-fixed coordinate system. Stride length depends on the step amplitude, the walking speed and the duration of the return stroke. Therefore, a comparison between those data and our crayfish results is only possible if temporal data on the duration of the power and return strokes are available. Similarly, when investigating curve walking in *Drosophila melanogaster*, Strauß and Heisenberg (1990) found changes mainly in the stride lengths of the inner legs. However, these data are also expressed in absolute coordinates. These authors do provide temporal values, but only for straight-walking animals. Therefore, no direct comparison is possible concerning the placement positions of the legs. Strauß and Heisenberg (1990) found no decoupling between contralateral legs, even for tight turns. Furthermore, during turning, *Drosophila melanogaster* shows lateral movements of the legs as well as nearly zero step amplitude in the hindleg. Such lateral movements have also been reported for the honeybee (Zolotov *et al.* 1975) and the escaping cockroach (Camhi and Levy, 1988). In the honeybee, the amplitude of the outer legs during turning seems to be increased, while the inner hindleg serves as a pivot. The agreement between these results and our findings for the crayfish may indicate that similar control strategies are used in insects and crustaceans.

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