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Role of the Trunk Musculature in Oviposition of the Carp, *Cyprinus carpio*

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Abstract Electromyograms were recorded from the lateral trunk musculature of ovipositing carp. At oviposition the muscles on both sides facing each other fired alternately, while those on the same side did almost simultaneously. The ovipositing actions of the carp are assumed to be simple, very rapid body bendings, closely resembling so-called burst swimming. The differences between the two actions could not be determined on electromyograms in this study.

In a previous study we recorded long lasting discharges from every part of the trunk musculature in ovipositing chum salmon and concluded that the fish extruded eggs solely by simultaneous contraction of the whole trunk musculature (Uematsu et al., 1980; Uematsu and Yamamori, 1982). Like the salmon, the carp belongs to a relatively primitive group of teleosts (Greenwood et al., 1966), but it possesses a hollow ovary covered with an elastic ovarian membrane. Therefore, conceivable power sources for oviposition are the trunk musculature and/or the ovarian membrane (Aronson, 1957; Hoar, 1957). However, the membrane by itself does not seem to be able to produce enough force to oviposit, since it is very thin and is poor in the muscular constituents (Uematsu, unpublished data).

According to Breder and Rosen (1966), the carp oviposits as many as hundreds eggs at a spawning, while dashing side by side with males on or among spawning substrates. This behavior is repeated until all the ovulated eggs are extruded. At each spawning act the fish beats tail several times. On the basis of this description and our observations of the spawning behavior of the carp, it is assumed that the ovipositing force is generated mainly by alternate rapid contractions of the trunk musculature on both sides.

The present study was undertaken to examine electro-myographically the trunk muscular activities of ovipositing female carp.

Materials and methods

Fish. Eight gravid females and a few mature males of the carp purchased from a local fish-farm were used. The females ranged from 290 to 470 mm in standard length. Fish were kept sexually separated till the experiment. Most females ovulated naturally, but some ovulated with gonadotropin (HCG) injection. Males were not treated. If the ovulated fish were left without courting males for a long period after ovulation, the fish released their eggs spontaneously. Therefore we checked fish at 4 a.m. every morning and electrodes were implanted to the ovulated fish.

Electrode implantation. After the fish was anaesthetized in a solution of 100 ppm MS-222, several pairs of electrodes made from enamel insulated copper wires of 0.2 or 0.3 mm in diameter and 1.8 m in length were implanted into the trunk muscles by a twin implanter. Electrode preparations and implantations were done after Hanyu et al. (1979) with some modifications. Leads of the electrodes implanted in the ventral muscles were run intramuscularly to prevent lead mutilations by males during the courtship behavior (Fig. 1). All the electrode leads were bundled and secured to the back just anterior to the dorsal fin, and the lead bundle was covered with a polyethylene or a silicon tubing to avert kink.

As shown in Fig. 1, the twin electrodes were implanted at four to six sites, which were selected among the left dark muscles (Ld), the left dorsal muscles (LD), and the anterior and posterior ventral (abdominal) muscles on both sides (LVa, LVp, RVa and RVp, respectively) of the fish's body.

The experimental tanks (2.0 or 2.7 m) were kept 25 cm deep by pouring well water. In

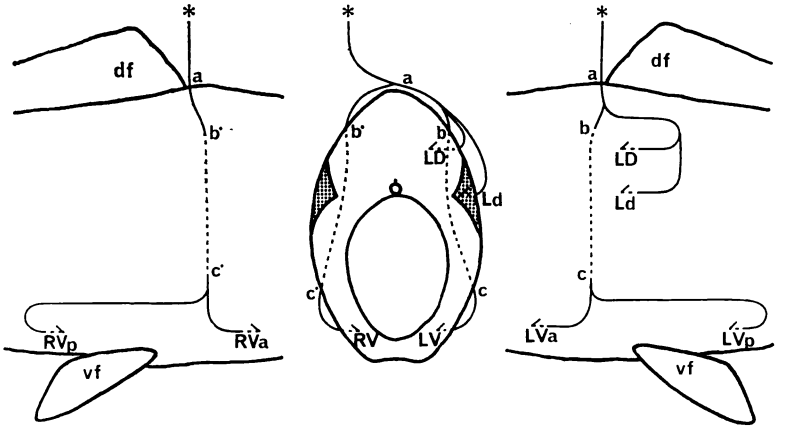

Fig. 1. Sites for electrode implantation (arrow heads) and routes of lead wires (solid and broken lines) of the experimental fish. The middle drawing shows the cross section through just anterior to the dorsal fin (df). A bundle of lead wires was secured to (a) position and lead wires implanted into the ventral muscles on both sides were run intramuscularly between (b) and (c), and (b′) and (c′). Stipplings indicate the dark muscles. Asterisks mean that this end was connected to amplifiers. Abbreviations: Ld, the left dark muscles; LD, the left dorsal ones; LVa, LVp, RVa and RVp, the anterior and the posterior ventral ones on the left and the right sides, respectively.

the tanks no spawning substrates were set to avoid tangling of the cable for recording electromyograms (EMG).

Electromyographic recordings. After the electrode implantation, treated female was placed in an experimental tank which had been previously occupied by two or three males. The same males were used throughout the season. Recording of EMG from the trunk musculature, led out extracellularly through bipolar electrodes, was made with a CRT oscilloscope (VC-9, Nihon Koden Co., Ltd.) equipped with a continuous photographing system. In some experiments a four channel data recorder (DFR-3515, SONY Corp.) was also used to record and reproduce EMG.

To record EMG during cruisings of sustained speeds and burst swimmings, a recirculating water tunnel (as described by Hanyu et al. (1979)) was employed. The fish used in this experiment was 265 mm in standard length.

Results

Immediately after entry of the female into the tank, at least one male began active courtship behavior during every experiment and within minutes a spawning act took place. Although the carp spawn among water-plants in the natural condition (Breder and Rosen, 1966), in this study fish always spawned against the side wall of the tank, since no spawning substrates were present there. Observed spawning behavior of carp are as follows. Males courted a slowly swimming female from behind to position parallel with her. Coming to the side wall, males pressed the female against it and consequently she was thrust up to the surface of the water. On that instance a spawning act occurred. They reiterated this sequence at intervals of a few minutes for 1 to 2 hours until all the ovulated eggs in the ovary were exhausted.

The trunk muscular EMG during the ovipositing acts could be recorded from all the eight females used (Figs. 2a, b and 3a–d). However, it was rather difficult to obtain good EMG which allow reliable analyses of muscular activities, because of violent base-line fluctuations caused by strong body movements of the ovipositing fish.

It was found that the fish used only the dark muscles during usual moderate swimming in the tank. No other muscles exhibited periodic excitations with duration and interval changing with swimming speeds (Fig. 2a–d).

On the other hand, at oviposition every part of the trunk musculature (not only the dark

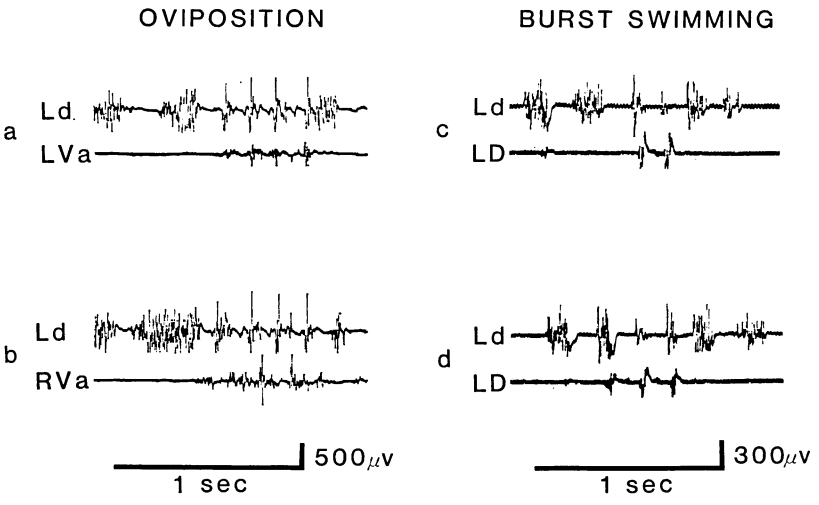

Fig. 2. Electromyograms recorded from an ovipositing fish (a and b) and a burst swimming fish (c and d). Constant periodic firings of the dark muscles (Ld) and cessations of the white muscles (LVa, RVa and LD) activities out of the two actions are remarkable. During both actions firing durations of the dark muscles also shortened. Abbreviations are as in Fig. 1.

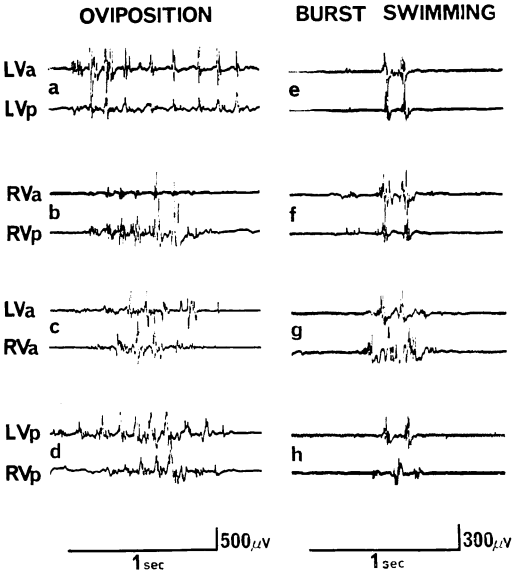

Fig. 3. Electromyograms recorded from an ovipositing fish (a–d) and from a burst swimming fish (e–h). Synchronous firings of the ventral muscles on the same side in an ovipositing fish (a and b) and in a burst swimming fish (e and f) are recognized. The ventral muscles on either side of the same body segment excited alternately in both actions (c, d, g and h). Abbreviations are as in Fig. 1.

muscles, but the white muscles) fired four times or more at a time (Figs. 2a, b, 3a–d). These firings superimposed on the base-line fluctuations coincided apparently with the observed tail beats at oviposition. Careful examination of EMG at oviposition revealed that the left and right ventral muscles of the same body segment excited alternately (Fig. 3c, d). In contrast, the anterior and the posterior ventral muscles of the same side fired almost simultaneously and the time lag between them could not be detected in this study (Fig. 3a, b), It was further noticed that the duration of dark muscle firings was also much shortened at oviposition (Fig. 2a, b).

The pattern of excitation in the muscles of ovipositing fish was compared with that in the fish swimming with bursts in the recirculating water tunnel. While swimming against a current over 3 body length/sec, the carp interposed a short burst frequently, which was accomplished by a few, faster tail beats. This action was represented by a sudden short discharge of large spikes, repeated less than 3 times, even at the recording sites which were silent in the fish swimming at moderate speeds (Figs. 2c, d, 3e–h). In this case, although the difference in EMG between the two actions could not be determined clearly, the anterior ventral muscles appeared to excite slightly prior to the

posterior ones, unlike an ovipositing fish. Furthermore, the duration of discharge in the dark muscles was markedly reduced, corresponding to the burst swimming (Fig. 2c, d).

Discussion

The carp ovary covered with the non-muscular ovarian membrane can not contract actively. Therefore, the main organs which produce the ovipositing force is conceivably the lateral trunk musculature (LTM), as is the same case with the chum salmon which has no closed ovary and oviposits solely with LTM (Uematsu et al., 1980; Uematsu and Yamamori, 1982). Accordingly we examined LTM activities of the ovipositing carp. However, contrary to our expectations, the electromyograms (EMG) recorded from the ovipositing carp were not so remarkable as those of the chum salmon.

At spawning the female beats her tail several times alongside with males just beneath the surface of the water. This motion was represented on EMG as a series of spikes with base-line fluctuations. Then LTM on both sides fired alternately, but firings of every electrode implanted muscle among the ipsilateral LTM took place almost simultaneously, implying that the ovipositing actions were nothing but simple, very rapid body bendings. It is naturally understood that the intraovarian, as well as abdominal, pressure increases when the fish bends her body. Hence, on every strong and quick twisting of the body the ovulated eggs seem to be extruded through the genital opening and then they are fertilized and scattered far and wide. Then, relaxation of the genital sphincter (Uematsu and Hibiya, 1983) will also occur. The ovipositing mechanism of the carp speculated here is rather primitive and less sophisticated than that of the chum salmon. But this seems very rational and is suited for the properties of the carp eggs, allowing wide scattering and good fertilization of numerous small adhesive eggs, though little by little in installments. Moreover it does not need other organs than LTM to oviposit eggs.

As in other teleostean fish, carp LTM is composed of mainly the white muscles and the dark ones (Johnston et al., 1977). Many electromyographic studies on the functions of teleost's LTM led the conclusion that the dark muscles accomplish the cruising of sustained speeds while the white muscles were active only during burst swimming (Rayner and Keenan, 1967; Hudson, 1973; Brill and Dizon, 1979; Freadman, 1979; Kashin et al., 1979). All these studies, however, dealt only with the dark muscles and the dorsal part of the white muscles. Therefore we had to conduct an experiment with a recirculating water tunnel to record activities of the ventral part of the white muscles during burst swimming, because the latter is thought to be effective for oviposition. The activities of every LTM during the two actions, oviposition and burst swimming, were basically similar. That is to say, both were shown on EMG as a series of short firings of EMG potentials. But there were some characteristic differences between them. First, each electrode-implanted muscle of an ovipositing fish contracted four times or more, but at a dash it fired only 2 or 3 times. Moreover, the heavier base-line fluctuations of EMG recorded from an ovipositing fish indicate that the body actions were greater than those of a dashing fish. These differences on EMG between the two actions were also represented on the spawning behavior observed with the naked eye. Despite the strong tail beats the ovipositing fish moved forward slowly for only a short distance, on the other hand dashing or burst swimming is a motion that propel fish forward quickly to escape from something or to catch bait. Some conceivable explanations may exist for this phenomenon that the ovipositing fish could not generate the effective thrust. One is that the body motion of ovipositing fish may not be such an undulatory movement of the body as to provide propulsive force during usual swimming (Bainbridge, 1958; Blight, 1977), but merely a swishing of the tail. Others are external causes; the tail may probably be exposed above the surface of the water, or female movements may be hindered by males or water plants. Although with the present study it is difficult to decide whether these explanations are correct or not, considering the differences in the muscular activities between the two actions, we are inclined to support the former reason. But, to determine this, a cinematographical study must be carried out.

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Literature cited

Aronson, L. R. 1957. Reproductive and parental behavior, pp. 271–314. *In* M. E. Brown, ed., The physiology of fishes. 2. Academic Press, New York.

Bainbridge, R. 1958. The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat. J. Exp. Biol., 35: 109–133.

Blight, A. R. 1977. The muscular control of vertebrate swimming movements. Biol. Rev., 52: 181–218.

Breder, C. M. and D. E. Rosen. 1966. Modes of reproduction in fishes. Nat. Hist. Press., New York, 941 pp.

Brill, R. W. and A. E. Dizon. 1979. Red and white muscle fibre activity in swimming skipjack tuna, *Katsuwonus pelamis* (L.). J. Fish Biol., 15: 679–685.

Freadman, M. A. 1979. Role partitioning of swimming musculature of striped bass, *Morone saxatilis* Walbaum and bluefish, *Pomatomus saltatrix* L.. J. Fish Biol., 15: 417–423.

Greenwood, P. H., D. E. Rosen, S. H. Weitzman and G. S. Myers. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Am. Mus. Nat. Hist., 131: 339–456.

Hanyu, I., K. Tsukamoto, K. Yamamori, P. V. Ngan, K. Furukawa and T. Hibiya. 1979. Simultaneous recording of physiological information from swimming fish. Bull. Japan. Soc. Sci. Fish., 45: 1261–1265.

Hoar, W. S. 1957. The Gonads and reproduction, pp. 287–321. *In* M. E. Brown, ed., The physiology of fishes. 1. Academic Press, New York.

Hudson, R. C. L. 1973. On the function of the white muscles in teleosts at intermediate swimming speeds. J. Exp. Biol., 58: 509–522.

Johnston, I. A., W. Davison and G. Goldspink. 1977. Energy metabolism of carp swimming muscles. J. Comp. Physiol., 114: 203–216.

Kashin, S. M., A. G. Feldman and G. N. Orlovsky. 1979. Different modes of swimming of the carp., *Cyprinus carpio* L.. J. Fish Biol., 14: 403–405.

Rayner, M. D. and M. J. Keenan. 1967. Role of red and white muscles in the swimming skipjack tuna. Nature, 214: 392–393.

Uematsu, K. and K. Yamamori. 1982. Body vibration as a timing cue for spawning in chum salmon. Comp. Biochem. Physiol., 72A: 591–594.

Uematsu, K. and T. Hibiya. 1983. Sphincter-like musculature surrounding the reproductive duct of some teleosts. Japan. J. Ichthyol., 30: 72–80.

Uematsu, K., K. Yamamori, I. Hanyu and T. Hibiya. 1980. Role of the trunk musculatures in oviposition of chum salmon, *Oncorhynchus keta*. Bull. Japan. Soc. Sci. Fish., 46: 395–400.

放卵中のコイから記録した体側筋筋電図

植松一真

コイの放卵は，筋成分に乏しい卵巣膜の構造からみて，体側筋によって行なわれると考えられる．そこで，産卵行動中のコイ雌魚からの体側筋筋電図の導出を試みた．

放卵時，体側筋（血合筋と普通筋）の各部からは，40～60 ミリ秒の短い叢放電が 4～8 回記録された．その際，同じ筋節レベルの左右の筋は交互に，また同側の体側筋はほぼ同時に活動した．このように，コイの放卵動作は突進時の遊泳動作に極めて類似していることが明らかとなったが，両動作の間に筋電図上の差違を見出すことはできなかった．これらから，コイの放卵動作は単純な魚体の屈曲にすぎないと推察された．すなわち，魚体が急速に屈曲される時に上昇する腹腔内圧によって，卵は卵巣内より体外へ押し出されるものと考えられる．

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