Eyestalk Musculature of the Crayfish, *Procambarus clarki*[1)]

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(*With 1 Text-figure and 1 Table*)

Introduction

Crustacean eyestalk has long been known to exhibit compensatory movement in response to the bodily tilt, and thus, its behavior has been subjects of a number of investigations. The movements of the eyestalk which are induced by optokinesis and by withdrawal reflex have also been subjected to various studies. Physiological analysis of these movements in relation to the central control necessitates a full description of the muscular arrangement. In Decapoda, the eyestalk musculature of a few Brachyura (Cochran 1953) and Reptantia (Parker and Rich 1893, Schmidt 1915, Paterson 1968) has been described. As to the Astacura of Reptantia, the most comprehensive study has been done on *Orconectes virilis* by Robinson and Nunnemacher (1966). Their observation has indicated that even in closely related species, there exist certain differences in the muscular arrangement as well as in number of muscles. This prompted us to study the eyestalk musculature of the crayfish, *Procambarus clarki*, of which visual as well as oculomotor responses have already been the subjects of number of investigations (Sandeman 1964, Wiersma and Yamaguchi 1964, Wiersma and Oberjat 1968, Hisada, Sugawara and Higuchi 1969).

Material and Method

Mature specimens of both male and female of the fresh water crayfish *Procambarus clarki* were studied. The eyestalks were isolated together with a dorsal anterior portion of the carapace. Excess part was trimmed off, until the entire eyestalk with the basal segment was isolated in van Harreveld's solution. Windows were made on the chitinous membrane at various places by removing small strips of chitin. The muscles were carefully

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exposed and were sometimes stained with methylene blue to have better demarcation of their boundaries. Fixed preparations were also used. Progressive fixation with 20% formalin and subsequent dissection recommended by Robinson and Nunnemacher (1966) was found very helpful. Cross-sectioning with quick frozen specimen was also employed to find out relative location of individual muscles.

Result

The muscles are primarily designated with numbers (Fig. 1). The names appearing in descriptions of each muscles are based upon the previous studies and/or determined by their geometrical arrangements. Exact functions of each individual muscles should be determined by more functional studies in living specimens, and the names used here should, therefore, be verified accordingly.

Muscle No. 1 and 2. These may be homologous to the medial retractors in *Orconectes* (Robinson and Nunnemacher 1966). These are two paired muscles lying side by side on the medial side of the eyestalk. More medial one (muscle No.

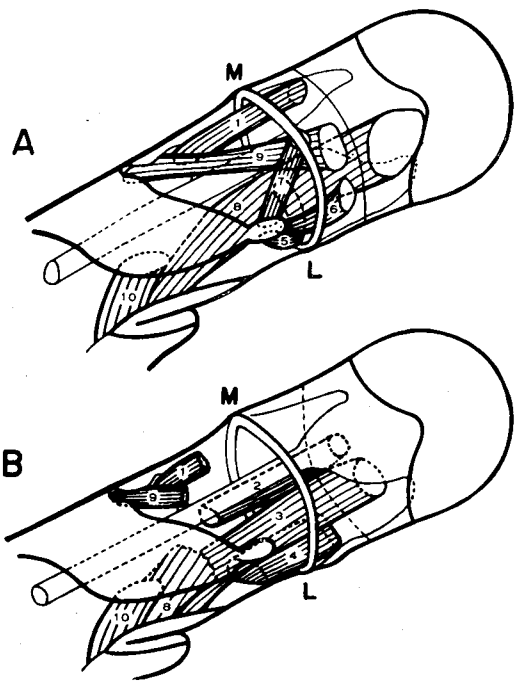

Fig. 1. Eyestalk musculature of *Procambarus clarki*, dorsal view of right eye. Dorsal (A) and ventral (B) musculature. M: antero-medial and L: postero-lateral orientation *in situ*. The eyestalk is slightly extended along its long axis at the arthrodial membrane in this figure. For details see text.

1) is originating from the medial extension of the relatively stiff chitinous membrane (sclerite) and the ventral one (muscle No. 2) is originating from the soft membrane slightly ventral to the sclerite. Both muscles insert in the eyecup just distally to the middle ridge of the inside of the distal segment. The muscle No. 1 consists only of several individual fibers which form a rather loose bundle. The second of the pair (muscle No. 2) has fibers which are thinner and more in number than the first one and lies more ventral. Their functions appear to be medial retraction of the eyestalk and also consequent slight abduction.

Muscle No. 3. The ventral retractor. A large, flat muscle originating from the ventral side of the basal segment just distal to the origin of the muscle No. 8. Its insertion is broad and lies at extreme distal of the eyestalk, beyond the middle ridge of the eyecup. The muscle lies immediately dorsal to the muscle No. 4, ventral depressor, and to the distal half of the muscle No. 5, lateral rotator.

Muscle No. 4. The ventral depressor. This is a short, flat muscle lying rather ventral and originates from the chitinous ridge of the ventral part of the basal segment and insert at the proximal side of the middle ridge of the eyestalk. Its function appears to be the slight depression of the eyestalk.

Muscle No. 5. The lateral rotator. Thin cylindrical muscle of peculiar placement. Its contraction will undoubtedly produce pure rotation of the distal segment, thus being characteristic in its single function when compared with others which are of more or less multifunctional. This muscle originates from the small sclerite protruding distally from the dorso-lateral roof of the basal segment, and runs parallel to the distal margin of the distal segment unlike any other muscles, and inserts at the ventral side of the margin of the distal segment. Its sole function appears to be dorso-medial rotation of the distal segment. The muscle counteracts to the dorsal member of the latereal retractor and the rotatory function of the muscle No. 8. The function may also be of synergist to the muscle No. 9.

Muscle No. 6 and 7. The lateral retractors. These are two muscles originating from the same chitinous sclerite from which the muscle No. 5 originates. Dorsal one (muscle No. 7) may be more properly described as being a rotator in function than a retractor. The contraction of this member will produce dorso-lateral rotation of the distal segment. Its insertion to the distal segment is at the dorsal proximal edge of the distal segment and almost perpendicular to the insertion of muscle No. 9. Lateral one (muscle No. 6) is short and runs parallel to the long axis of the eyestalk, inserting at the proximal side of the middle ridge of the distal segment. The function may be of slight abduction of the distal segment.

Muscle No. 8. The abductor. This is the largest of ten eyestalk muscles, its fibers are thick and runs twisted along the entire length. The origin is ventral and slightly lateral and also close to the middle of the basal segment. The insertion is latero-dorsal at the distal half, and beyond the middle ridge of the

distal segment. The contraction of this muscle results in abduction of eyestalk and in possible rotation of the dorsal side laterally, because of the twisting of constituting fibers and also of the oblique setting of the origin and the insertion.

Muscle No. 9. The dorsal retractor. This is an obliquely placed cylindrical muscle originating from the medial chitinous extention of the basal segment, inserting to the almost dorso-lateral roof of the distal segment just proximal to the middle ridge. The originating point is just proximal to the medial retractor (muscle No. 1). The contraction of the muscle will produce both the medial retraction and the medial rotation of the dorsal side of the eyestalk, thus resulting in a dorsomedial rotation of the eyestalk. The function therefore appears to be of the antagonist to the muscle No. 7, No. 8 and No. 10.

Muscle No. 10. The attractor. This is a short, thick muscle located in the basal segment of the eyestalk, and originates from the ventral floor of the chitinous basal segment. This muscle runs upward in the lateral half of the eyestalk and insert at the roof of the basal segment slightly laterally beyond the cleft which is dividing the rigid roof and the floor of the basal segment at the lateral side. The contraction of this muscle will lessen the width of the cleft and thus rotate the dorsal side of the eyestalk slightly laterally.

Remarks

In general, fundamental muscular arrangement in the eyestalk of *Procambarus clarki* showed a close similarity to that of the another Astacura, *Orconectes virilis* which has been described by Robinson and Nunnemacher (1966). The number of muscles of these two species are compared in Table 1.

Table 1. A comparison of the eyestalk muscles of *Procambarus*, with comparable muscles in *Orconectes*.

	Procambarus clarki	*Orconectes virilis*
Dorsal Retractor	1 (No. 9)	1
Ventral Retractor	1 (No. 3)	1
Lateral Retractor	2 (No. 6, 7)	(2) branches
Medial Retractor	2 (No. 1, 2)	2
Lateral Rotator	1 (No. 5)	1
Ventral Depressor	1 (No. 4)	2
Abdutor	1 (No. 8)	1
Attractor	1 (No. 10)	1

The most remarkable difference in geometry of muscles between these two species may be found in the dorsal retractor (muscle No. 9). In *Orconectes* this eyestalk retractor is flat, very long and lies in parallel with the long axis of the eyestalk, so the rotatory function is hardly expected in this muscle, whereas in

Procambarus, the retractor (muscle No. 9) is cylindrical, not so long at normal position of the eyecup, projecting obliquely from medial terminal toward the dorsal part of the eyecup, and supposed to be activated synergetically with the lateral rotator (muscle No. 5) when the eyestalk turns along its long axis in dorsal to medial direction.

Another difference in features was found in the depressors of these two species. Two separate individual eyestalk depressors lying side by side have been described in *Orconectes* by Robinson and Nunnemacher (1966), whereas such clear separation of muscles could not be found in *Procambarus*. In the latter species, however, there exist a rather considerable individual variation of the muscle width as well as the density of muscle fibers. In the specimen of which depressor is relatively loose, this muscle may be seen to be separated partially along its long axis into two or more subbundles.

The third difference lies in the lateral retractors. Robinson and Nunnemacher (1966) described in *Oroconectes* the single retractor which divides almost immediately into two branches. Our observation indicates, in *Procambarus*, two separate retractors originate from separate points on the sclerite. The functions of these two retractors seem to be also distinctly different, the dorsal one (No. 7) is more of the rotator while the lateral one is more pure in retracting function.

It should be the one of the most important properties of the eyestalk musculature that no single muscle can be regarded to function separately in this kind of complicated muscular arrangement, and that any movement of the eyestalk should certainly be brought out by coordinative and consorting actions of more than one and up to several muscles. In this sense, there exist no definite synergistic or antagonistic relations between any pair of the muscles.

These facts imply that the coining of any functional name to an individual muscle is rather misleading and must be, if possible, done ultimately after thorough understanding of the mechanism of the eyestalk movements. Thus the adequacy of the functional names used here should be regarded as being limited accordingly.

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Summary

Ten oculomotor muscles were found in *Procambarus clarki*, and classified into following 8 groups by possible functions deduced from their arrangements in the eyestalk: dorsal retractor, ventral retractor, lateral retractors (two muscles), medial retractors (two muscles), lateral rotator, ventral depressor, abductor and attractor.

General arrangement shows close similarity to that of *Orconectes virilis*, except the presence of the two lateral retractors and absence of the second depressor.

Structural arrangement indicates that any single muscle does not seem to function separately and there is a strong indication of any eyestalk movement to be produced by their consorting actions.

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