

Neurobiology of the Anomura: Paguroidea, Galatheoidea and Hippoidea

DOROTHY HAYMAN PAUL

Department of Biology, University of Victoria, Box 3020, Victoria, BC V8W3N5, Canada (dhp@uvvm.uvic.ca)

Abstract

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Anomurans are valuable subjects for neurobiological investigations because of their diverse body forms and behaviours. Comparative analyses of posture and locomotion in members of different families reveal that peripheral differences (in skeleton and musculature) account for much of the behavioural differences between hermit crabs and macrurans (crayfish), squat lobsters and crayfish, hippoid sand crabs and squat lobsters, and albuneid and hippid sand crabs, and that there are correlated differences in the central nervous systems. The order of evolutionary change in discrete neural characters can be reconstructed by mapping them onto a phylogeny obtained from other kinds of data, such as molecular and morphological. Such neural phylogenies provide information about the ways in which neural evolution has operated. They are also useful in developing hypotheses about function of specific neural elements in individual species that would not be forthcoming from research on single species alone. Finally, comparative neurobiological data constitute a largely untapped reservoir of information about anomuran biology and anomuran relationships that, as more becomes available, may be helpful in systematics and phylogenetics.

Keywords

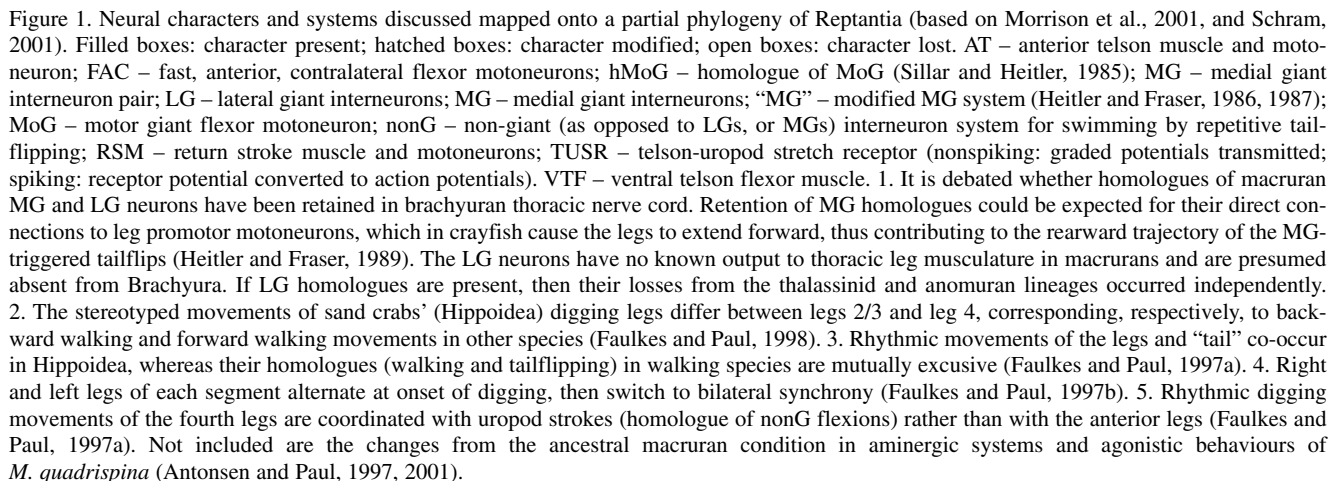
Crustacea, Anomura, neurobiology

Introduction

The diversity of body forms and behaviours that have evolved within the Anomura (Fig. 1) offer neurobiologists numerous opportunities to examine variants in form and function in identified neurons and neural circuits mediating specific movements or elements of behaviour and the relationships between them. This is because discrete and identifiable neural differences are expected to underlie inter-specific differences in behaviour ranging from single movements of individual appendages to agonistic interactions. The variants in amplitude and order of pereopod joint movement during locomotion or posturing during social encounters, or in the social behaviours themselves, may therefore be viewed as the results of natural, as opposed to invasive, experiments to manipulate different neurophysiological and neuroanatomical parameters in the nervous system of one taxonomic group (Antonsen and Paul, 1997, 2000, 2002; Faulkes and Paul, 1997b, 1998; Paul, 1991). In addition to investigating mechanistic issues in neuroscience, such comparative research can begin to address such fundamental questions in evolutionary neurobiology as: How conservative are neurons and neuronal circuits? Are some morphological and physiological features more easily (i.e., often) modified than others during behavioural evolution? What constraints on changing complex neuronal networks are imposed by the necessity that they remain functional through

speciation? We are far from achieving definitive answers to any of these questions, particularly the last one, but the comparative data on the neurobiology of some anomurans summarized here indicate the direction toward which the answers are likely to lie. From an entirely different perspective, comparative research on adult and embryonic nervous systems can provide taxonomists and evolutionary biologists with useful characters to supplement other types of data used to construct phylogenies (Breibach and Kutsch, 1995; Harzsch and Waloszek, 2000; Sandeman and Scholtz, 1995; Scholtz and Richter, 1995; Strausfeld, 1998; Whittington, 1995; Whittington and Bacon, 1997). This is because nervous systems are relatively conservative through evolution (compared with other internal tissues and organ systems), although not to the degree once thought (Whittington, 1995; this review). Species differences between identified neurons and neural connections can be recognized because they stand out against a background of highly conserved neural architecture. Most comparative work has been at higher taxonomic levels, and the Anomura, considering their diversity, are under-represented even in studies focusing on Decapoda.

Comparative neurobiological research. Neurons and neurobehavioural circuits do not fossilize, which makes recognition of modern surrogates for ancestral neural traits essential for an understanding of nervous system evolution. In external



morphology and modes of locomotion, galatheids most closely resemble macruran reptantians, such as crayfish. The external form of crayfish, particularly of the abdomen and tailfan, is similar to that of the early fossil decapod *Paleopalaemon newberryi* (Schram et al., 1978). Similar morphology suggests similar behaviour, in this case, posture and uses of the “tail”, making neurobiological data on sensory and motor systems in crayfish for the most part suitable surrogates for the ancestral decapod condition. Therefore, regardless of specific phylogenetic relationships, many neurobiological features of crayfishes may reasonably be considered surrogates for the ancestral condition of homologous features in anomurans (Paul, 1989a, 1991; Paul et al., 1985, 2002).

Anomuran neurobiology

Anomurans have, by definition, modified the ancestral macruran reptantian “tail” (abdomen and tailfan). The most obvious correlated neural difference from their macruran ancestors is fusion of the first abdominal with the last thoracic ganglia, leaving five free abdominal ganglia in the “tail”, the homologues of macruran abdominal ganglia 2 through 6. The cytoarchitecture of abdominal ganglion 1 in galatheids and hippoids has not substantially changed, however, so that identification of homologues of its neurons with those in the more posterior abdominal ganglia, as well as with neurons in macruran abdominal ganglia, is relatively straightforward (Antonsen and Paul, 2001a; Mittenthal and Wine, 1978; Wallis et al., 1995; Wilson and Paul, 1987). Nineteenth and early twentieth century neurobiologists (or, in the vocabulary of the time, zoologists, anatomist, physiologists) described a plethora of interesting features about crustacean, including some anomuran, behaviours and nervous systems (see references in Bullock and Horridge, 1965), many of which could profitably be revisited with modern research tools. For example, Alexandrowicz (1951, 1952, 1954), through unparalleled use of methylene blue staining, described details of dorsal muscle receptor organs (analogues of mammalian muscle spindles) in numerous crustaceans, including pagurids. Alexandrowicz’s exquisite illustrations fostered pioneering electrophysiological work on these sense organs which continues today (Macmillan, 2002; Macmillan and Patullo, 2001; Pilgrim, 1960).

Although most often studied in macruran decapods (Macmillan, 2002), bilateral pairs of segmentally arranged muscle receptor organs (MRO) are present in Hoplocarida (Alexandrowicz, 1954) and Syncarida (Wallis, 1995) and, therefore, presumed ancestral in Malacostraca. Further investigation of the MROs that have been described in galatheid squat lobsters (Pilgrim, 1960; Wallis et al., 1994) and pagurid species (Alexandrowicz, 1952; Pilgrim, 1960, 1974), as well as investigations in other anomurans, are certain to provide insight into how evolutionary modifications in this array of ancient sense organs contribute to the distinctive postures and forms of locomotion in the Anomura (Wallis et al., 1994).

Motor systems – from familiar to novel forms of posture and movement. The paired, dorsal, medial giant (MG) and lateral giant (LG) interneurons in the nerve cords of macruran species

and hermit crabs were the first neurons in crustacean central nervous systems to be recognized as re-identifiable neurons (see references in Bullock and Horridge, 1965); investigations of their physiology, inter-connections with other neurons, roles in locomotion, and, more recently, in agonistic behaviours in crayfish continue to inform us about how crustacean behaviours are mediated, as well as about general mechanism of nervous system function (Edwards et al., 1999; Wine, 1984). Crayfish’s MG and LG neurons, with associated motor giant and segmental giant neurons, coordinate the rapid and powerful flexions of the abdomen-tailfan called tailflips (Edwards et al., 1999; Wine, 1984). Anomurans have modified (Paguroidea) or lost (Galatheaidea, Hippoidea) these giant interneuron systems (Fig. 1). Only the MG system, including the segmental and motor giant neurons, is retained, with modifications, in pagurids to subserve their new mode of escape: rapid withdrawal into their gastropod shell (Chapple, 1966; Heitler and Fraser, 1986, 1987; Umbach and Lang, 1981). Some repercussions in the pagurid nervous system of acquiring a hydrostatic skeleton, asymmetrical abdomen, and use of the last two pairs of pereopods to transport gastropod shells for shelter have been investigated (Bent and Chapple, 1977; Chapple, 1966, 1969 a, b, c, 1973; 1993; Chapple and Hearney, 1976; Herreid and Full, 1986), but many interesting questions remain, such as the control of the tailfan’s grip on the shell and of the asymmetric swimmerets, when present. The partial reversion to tailfan symmetry in pagurid species using straight shells (Imafuku and Ando, 1999) has likely engendered some modifications in the muscles and reflex control of the “tail” from those in pagurids hoisting spiraled shells (see Chapple, 1966, 1969b, 1973); are they reversions to the macruran condition or new permutations of the asymmetric sensory – motor systems of other pagurids? The retention of the MG interneurons and related circuitry in pagurids (also in Thalassinidea: Bullock and Horridge, 1965; Paul, pers. obs.) illustrates that evolutionarily conserved neuronal networks can retained the ability to coordinate movements in the face of substantial alterations in peripheral, skeleto-muscular systems.

Galatheaidea and Hippoidea have apparently lost both MGs and LGs (Sillar and Heitler, 1985; Paul, 1991; Wilson and Paul, 1987). However, both perform repetitive tailflipping, rapid extensions-flexions of the “tail”, such as used by crayfish for swimming, and which are presumably mediated by homologues of crayfish’s non-giant circuitry for swimming (this circuitry is called non-giant, nonG, because neither MGs nor LGs are involved) (Paul, 1981a, 1991; Sillar and Heitler, 1985; Wilson and Paul, 1987). Unexpectedly, the two squat lobster species that have been investigated differ in their complement of fast flexor motoneurons, although their tailflipping behaviours appear to be indistinguishable (Fig. 1). In *Galathea strigosa*, the clusters of fast flexor motoneurons are similar to those in crayfish, including homologues of crayfish’s segmentally repeated motor-giant motoneurons (Fig. 1, hMoG) which have, however, lost the specialized features associated with electrical coupling to the giant interneurons and become morphologically similar to other fast flexor motoneurons (Sillar and Heitler, 1985). *Munida quadrispina*, by contrast, has not only lost motor-giant homologues but also the entire cluster of

anterior contralateral fast flexor motoneurons (Wilson and Paul, 1987). Since no functional or behavioural correlates of these neural differences are evident, it appears that evolutionary changes in nervous systems during speciation occasionally occur independently of altered morphology or behaviour. Such events would leave overtly similar sibling species with different potential for subsequent neurobehavioural evolution. Other squat lobsters should be investigated to determine whether these data are representative of these genera, in which case they would suggest that *Munida* is more derived than *Galathea*.

Porcelain crabs (Porcellanidae) flap their small, flat abdomens rhythmically to swim upside down (Hsueh et al., 1998) and to stabilize their descent to the bottom after dropping off vertical surfaces (Paul, pers. obs.). This is presumably a reduced form of the vigorous swimming movements exhibited by Galatheidae and crayfish, and therefore homologous to non-giant tailflipping. Nothing is known about the musculature, motoneurons, or the central circuitry executing this porcellanid behaviour, but it is an almost certainty that porcellanids lost MoG, as have *M. quadrispina* and the Hippoidea, rather than transferred them into ordinary fast flexor motoneurons, as occurred in *G. strigosa* (hMoG in Fig. 1).

Non-giant tailflipping was also retained in both families of sand crabs (Hippoidea; Fig. 1). In albuneid species, this is evident as the tail-“flapping” they use, along with rowing movements of their pereopods, to swim awkwardly upside down – like porcelain crabs described above – (Paul, 1981a) as well as to assist the pereopods when digging into sand (Faulkes and Paul, 1997a, b, 1998). The retention of non-giant tailflipping in hippid sand crabs is less obvious, because they keep their abdomen flexed beneath them and beat their highly modified uropods rapidly both to swim (Paul 1971, 1981a) and assist the pereopods in digging (Faulkes and Paul, 1997a, b, 1998). Homologies between individual muscles in sand crabs and other decapod species have been confirmed by examination of their innervations, specifically the locations and morphologies of the motoneurons innervating them, which are highly conserved (Paul, 1981b; Paul et al., 1985), but evidence for the homology of hippids’ swimming-by-uropod-beating and tailflipping is indirect but substantial: numerous similarities between motor patterns and between homologous motoneurons activating functionally divergent, homologous muscles (Paul, 1981a, b, 1991; Paul et al., 1985; Fig. 1). Direct tests of this hypothesis will require comparison of the neuronal circuits for these two behaviours, and little is known about either of them, other than that both rely on central pattern generation (Paul, 1979; Reichert et al., 1981; see *Discussion*).

Much of the difference in form between uropod beating and tailflipping can be accounted for by biomechanical differences, due to changes in the uropod articulation and the telson-uropod musculature in hippids (Paul, 1981a, b, 1991; Paul et al., 1985). However, hippids’ superb adaptation to life in the swash zone of exposed sandy beaches, where they are tireless swimmers and champions for speed among burrowing species (Dugan et al., 2000), required two evolutionary novelties in addition to rearrangements and modifications of ancestral neural and muscular traits: a muscle and a stretch receptor. The uropod

return-stroke muscle in the telson, innervated by three motoneurons (two excitatory, one inhibitory), occurs only in hippids (Paul et al., 1985); it is very small in albuneids, but has become one of the largest muscles in the body of hippids. Without it, the large return stroke movement of the uropod in hippids would be impossible (Paul, 1981b; Paul et al., 1985). This new movement is monitored by a new telson-uropod stretch receptor that is unique to hippids.

Novel stretch receptors. Telson-uropod stretch receptors (Fig. 1, TUSR) are found only in squat lobsters (Galatheidae) and sand crabs (Hippoidea) (Maitland et al., 1982; Paul, 1972; Paul and Wilson, 1994; Wilson and Paul, 1990). They are close and approximately parallel to the anterior Telson-Uropodalis muscle (= the hippid Dorso-Medial muscle), which is relatively larger than its homologue in macrurans and occupies the space in the anterior telson vacated by the loss of the macruran Anterior Telson muscle (Paul et al., 1985). The sensory neurons of the TUSRs are unusual because they are monopolar and their somata are located in the last, sixth abdominal, ganglion of the ventral nerve cord; i.e., their central morphology, like that of similar stretch receptors associated with the macruran swimmerets and macruran and brachyuran pereopods, resembles that of motoneurons (Bush, 1976). Typical mechanosensory neurons in arthropods are bi- or multipolar and their cell bodies lie outside the central nervous system, close to the periphery. Telson-uropod stretch receptors apparently evolved twice, first in the galatheid-hippid common ancestor and again in hippids. Alternatively, the first telson-uropod stretch receptor could have evolved prior to the paguroid divergence and was subsequently lost in hermit crabs. The TUSRs in *Galathea strigosa*, *Munida quadrispina*, and *Blepharipoda occidentalis* (Maitland et al., 1982; Paul and Wilson, 1994) and *Lepidopa californica* (Paul, pers. obs.) are morphologically and physiologically very similar and presumed homologues. The central location and morphology of their sensory neurons are similar, and these neurons generate conventional action potentials when their peripheral dendrites are stretched by elevation of the uropod (Maitland et al., 1982; Paul and Wilson, 1994). No comparable proprioceptors monitoring movement of the basal joint of the uropod have been found in any macruran or pagurid, which suggests that the greater freedom of movement of the uropods in galatheoids and hippids (Paul et al., 1985) may have made the evolution of a proprioceptor to monitor whole limb movement advantageous. The abdomen-propodite chordotonal organ in the uropod of crayfish originates from the third nerve of the sixth abdominal ganglion as this nerve enters the uropod (Field et al., 1990). Since its proximal attachment is flexible, this receptor would be unsuited to monitoring movement across the much more mobile articulation of the uropod with segment 6 in squat lobsters and sand crabs (Paul et al., 1985), and no anomuran homologue of this crayfish stretch receptor has been found.

The hippid telson-uropod stretch receptor (examined in detail in *Emerita analoga* and *E. talpoida*: Paul, 1972; Paul and Bruner, 1999; Wilson and Paul, 1990, and anatomically identical in *Hippa pacifica* and *E. austroafricanus*: Paul, pers. obs.) is in a comparable position to the TUSRs in the tailflipping

anomurans and it, too, responds to uropod elevation and, in particular, the uropod remotion brought about by contraction of the return-stroke muscle, unique to hippoids and much enlarged in Hippidae, as described above. However, the different positions of the somata and projections of the neurites of the sensory neurons in the sixth abdominal ganglion are strong evidence that the TUSRs in hippids and the tailflipping anomurans (Albuneidae, Galatheidae) are not homologues (Paul and Wilson, 1994). The hippid sensory neurons are also physiologically dissimilar: they are nonspiking, that is, they are incapable of generating action potentials, as can the galatheids and albuneid receptors, but instead transmit afferent signals in the form of graded depolarizations which mimic in form and amplitude the stretch applied to the receptor strand (Paul and Bruner, 1999). Apparently the transformation of the stem (albuneid-like?) hippoid tailfan into the extraordinary tailfan of hippids (Paul et al., 1985) included the replacement of the ancestral, spiking telson-uropod stretch receptor by a new one that ostensibly serves the same function, that is, sensing elevation of the uropod and activating resistance reflexes in homologous uropod muscles. The caveat here, however, is that the functional details, behavioural roles, and synaptic connections are still poorly understood for any of these receptors. Nevertheless, it appears that during hippid evolution, the spiking sensory neurons of the receptor in their tailflipping ancestors were not converted to nonspiking neurons, as was initially assumed (Bush, 1976; Paul, 1991). Paul and Bruner (1999) discuss the hypothesis that evolution of the physiological properties of these nonspiking sensory neurons may have been determined by their interconnections with nonspiking cells in the central pattern generator for swimming. Observations from two lines of research in other reptantians suggest this hypothesis. One is that certain swimmeret motoneurons are coupled to swimmeret interneurons in their hemiganglion (Heitler, 1978; Paul and Mulloney, 1985). The second is that nonspiking stretch receptors morphologically similar to those in hippids are interconnected with the pattern generators for the limb whose movement they monitor (thoracic walking legs: Sillar and Skorupski, 1986; abdominal swimmerets: Paul, 1989b). Whatever the adaptive drive for the unusual physiological properties of the hippids' sensory neurons, the repeated appearance of telson-uropod stretch receptors in Anomura demonstrates that new types of neurons can be added to inherited sensory-motor systems in the course of behavioural evolution.

Modular nervous systems and central pattern generators. The evolutionary potential of segmental body plans has long been recognized, and the ontogenetic mechanisms by which segmental characters may be selectively lost, added, moved, or modified are becoming apparent through the applications of genetic and molecular techniques to a variety of taxa amenable to such research (Giribet et al., 2001). Unfortunately, anomurans, indeed most crustaceans, are not among the latter, primarily due to their complex life cycles. But fortunately, their segmental nervous systems are amenable to detailed morphological and physiological analyses, which allow detailed comparative investigation of the neural substrates for their

divergent behaviours. Much of this material has been recently reviewed (Paul, 1991; Paul et al., 2002), so here I will highlight a few of the issues and refer readers to the research publications for substantive details and further discussion.

Neural networks driving repetitive movements such as underly locomotion, respiration, chewing, and other rhythmic behaviours have at their core central pattern generators (pace-maker neurons or small assemblies of neurons). The best known are the central pattern generators of the stomatogastric nervous system in crustaceans (Harris-Warrick et al., 1992). The stomatogastric system is clearly an ancient network that has been largely conserved morphologically. Variations in physiological details (synaptic properties, neuromodulators, etc.) have been uncovered, but not extensively investigated in the context of anomuran phylogeny or in relation to the ecology and habits of different species (Katz and Harris-Warrick, 1999). Paired segmental pattern generating modules control the limbs of crustaceans, each limb being under the control of the adjacent hemiganglionic center (Mulloney and Hall, 2000; Murchison et al., 1993). Much less is known about cellular composition and network operations of these hemiganglionic centers than about the stomatogastric system. They clearly differ in cellular composition – local interneurons, many nonspiking, form the core of the motor pattern-generating network, rather than motoneurons, as in the stomatogastric nervous system, nevertheless largely similar mechanisms appear to be used (e.g. graded potential, reciprocal inhibition, multiplicities of ion channels with differing kinetics). Testable hypotheses about species differences can be formulated, therefore, even without complete knowledge of the particular pattern generators in question.

Divergences in pereopod use in posture and locomotion in galatheids and hippoids, accompanying modifications in thoracic segmental morphology and endophragmal skeleton, have been correlated with specific alterations in musculature, motoneurons, and motor patterns in various studies (Antonsen and Paul, 2000; Faulkes and Paul, 1997a, b, 1998). Each segmental ganglion in the ventral nerve cord of crustaceans contains a pair of central pattern generating circuits (one/limb) (Mulloney and Hall, 2000; Murchison et al., 1993). Interneuronal connections between hemiganglionic centers allow bilateral and longitudinal coordination of motor activity produced by these hemiganglionic centers (Namba and Mulloney, 1999). The evolutionary potential of this functionally flexible arrangement has been exploited extensively in the evolution of the hippoid digging behaviour, a mosaic derived by amalgamation of two disparate forms of ancestral locomotion, walking and non-giant tailflipping (Faulkes and Paul, 1997a, b, 1998). Later divergences of phase couplings among the digging legs and between the legs and “tail” accompanied divergence of the two sand crab families, Albuneidae and Hippidae (Faulkes and Paul, 1997a, b, 1998; Fig. 1).

Comparative neurobiological studies of other anomuran behaviours are likely to provide inferences about how modular systems of neurons function and evolve, as well as illuminating the biology of the Anomura per se. For example, the modified posture and gait of hermit crabs, associated with their asymmetrical abdomen and transport of gastropod shells into

which they “retreat” rapidly (Chapple, 1966, 1973; Herreid and Full, 1986), must have entailed changes in pereopod neuromusculature and its central control. These remain to be explored. Snow’s (1975a, b) study of antennular flicking in pagurids could also be profitably pursued. One may suppose that flicking is underlain by hemiganglionic pattern-generating circuitry similar (serially homologous) to that controlling pleopods and pereopods (Murchison et al., 1993).

The basal musculature of crustacean limbs is often extremely complex and may include muscles with multiple heads and specialized functions. Divergence in segmentally repeated neuromuscular elements between segments in one species and in the same segment in different species clearly contributes to the postural and locomotory peculiarities of individual species. This is illustrated by the study of Antonsen and Paul (2000) on the leg depressor muscle in *M. quadrispina*, which highlights the need for more, detailed analyses of the functional morphology and innervation of such muscles, including the central structure of their motoneurons, in order to understand how the central neural networks (and neuromodulators, see below) produce species characteristic behaviours.

Neuromodulation and social behaviours. Hormones and neuro-modulators regulate the expression of the moment-to-moment behaviours produced by sensory-motor systems emphasized in this review. They confer functional, as well as evolutionary, flexibility on neurobehavioural networks (Katz and Harris-Warrick, 1999). The involvement of serotonin and octopamine in agonistic behaviours of crayfish and other crustaceans is well known (Huber et al., 1997), but an understanding of the sites and mechanisms of action of these biogenic amines is very incomplete (Panksepp and Huber, 2002). Unlike crayfish, *Munida quadrispina* (Galatheididae) neither form social hierarchies nor fight, although during agonistic encounters, they perform rather stereotyped gestures and behaviours that resemble those performed by dominant and subordinate crayfish (Antonsen and Paul, 1997). Nevertheless, as in crayfish, injection of controlled doses of serotonin or octopamine into the hemolymph of *M. quadrispina* induces, respectively, “dominant” or “subordinate” gestures and behaviours in isolated animals (are they displaying to a phantom conspecific?). Most remarkably, serotonin-injected animals engage in full-blown fights when paired with an un-injected individual (which tries, unsuccessfully unless rescued by the experimenter, to retreat) (Antonsen and Paul, 1997). Evidently *M. quadrispina* have not lost the “fight center”, but the “interest in fighting”, perhaps due to the loss of a particular synapse or expression of a serotonin (or other) receptor at some critical point in the circuitry involved in controlling agonistic behaviour (Antonsen and Paul, 1997). Information on the social behaviours of other galatheid genera is largely lacking, and circumspection should be used in interpreting differences in cheliped length, or other morphological characters, as indicators of a species’ agonistic behaviour (Creasey et al., 2000). Comparisons of immunocytochemical maps of serotonergic and octopaminergic neurons reveal both striking similarities and discrete differences between these systems in *M. quadrispina* and crayfish,

demonstrating that conserved and modified components of neuro-modulatory networks can be identified (Antonsen and Paul, 2001, 2002). Much more research is needed to clarify the functional organization of these aminergic systems and their interconnections with the rest of the nervous system in *M. quadrispina*, and other anomurans should be similarly investigated. The variants in social behaviour evident among anomuran species constitute a largely untapped source of information about mechanisms of neuromodulation and their evolution.

Discussion

By placing the neural characters discussed above on a partial phylogeny of the Reptantia which includes anomurans’ closest relatives (Fig. 1), several suppositions about neurobehavioral evolution in Anomura can be drawn. This exercise also both highlights under-studied groups and suggests experimentally testable hypotheses about specific neuronal systems in particular species. The seven characters listed at the base, with the possible exception of nonG (the circuitry for repetitive tailflipping that does not involve either sets of giant interneurons), are ubiquitous among macruran decapod groups, including natantian taxa (Paul, 1989a; Paul et al., 1985), although they are most fully described in astacidean species, primarily of crayfish (Wine, 1984). These characters are not equivalent in that some are individual neurons, whereas others are neuronal systems identified by their mediation of specific behaviours; few re-identifiable neurons in the latter have been described, but as they become known, they will constitute additional characters that will be useful for analysis of neuro-behavioural evolution or in phylogenetic reconstructions. The losses preceding and accompanying the divergence of the anomuran groups included major elements of macrurans’ startle/escape systems (one or both of the giant interneurons – see Fig. 1 footnote 1), as well as certain components of the massive tail neuromusculature, and were seminal for the anomuran radiation (Paul et al., 1985). In particular, the demise of both LG and MG interneurons in Galatheoidea and Hippoidea would have reduced constraints against modification of tailfan form, neuromusculature, and central motor systems controlling locomotion that were present in their macruran ancestors (Paul et al. 1985, 2002). This permitted the diversification of morphology and behaviour so evident in galatheid and hippoid anomurans.

The number of evolutionary modifications of retained neural characters (hatched boxes in Fig. 1) is clearly a gross underestimation, because, as explained above, most are functional neural networks (e.g., the nonG circuitry for swimming, the CPGs, central pattern generators, producing rhythmic limb movements) in which an unknown number of neuronal and synaptic changes are likely to have occurred, but remain to be identified. One additional change in tailfan neuromusculature not yet mentioned or included in Fig. 1 was pivotal to the evolution of the hippid sand crabs’ novel mode of swimming by beating the uropods. This was the conversion of an axial muscle into an appendage muscle by changing its insertion: in all tailflipping species (including galatheids and albuneids), the PTF (posterior telson flexor) muscle is the terminal member of

the concatenated series of fast flexor muscles that mediate the abdominal flexions or power strokes in tailflips (Dumont and Wine, 1987). The PTF homologue in hippid sand crabs inserts on the ventral rim of the uropod coxa, adjacent to the insertion of the uropod power-stroke muscle (homologue of the macruran posterior telson-uropodalis muscle), so that, rather than flexing the telson on the abdomen, it assists in uropod promotion during uropod beating (Paul et al., 1985). The homology between components of the power-stroke neuromusculature (muscles and motoneurons) for uropod beating and tailflipping provides substantive evidence for the homology of the neural circuitries for swimming by uropod beating and tailflipping (Fig. 1: nonG→uropod beating). This hypothesis originated with the observation that at high frequencies of uropod beating, a small extension of the anterior abdomen occurs with each uropod return stroke (= extension phase of tailflipping; Paul, 1971). Further support for the hypothesis of homology of these dissimilar behaviours is that rhythmic bursting of the motoneurons innervating the PTF homologue in hippids is very prominent in the uropod motor pattern generated by isolated nerve cords of *Emerita analoga* (Paul, 1979); i.e., uropod beating, like nonG tailflipping (Reichert et al. 1981), is organized by a central pattern-generating circuit that does not require sensory feedback to sustain its generation of alternating activity in power-stroke (flexion) and return-stroke (extension) motoneurons. Regardless of the validity of this hypothesis, the evolution of hippids' novel mode of swimming combined the considerable evolutionary flexibility in behaviour permissible by peripheral changes in skeleto-musculature with the evolutionary potential derived from crustaceans' complex neuromusculature (Paul et al., 1985; Antonsen and Paul, 2000).

The extent and nature of alterations in inherited networks into which new neural elements have been incorporated (Fig. 1, black boxes in anomuran portion of the tree) are as yet unexplored. Some may have been minimal: the uropod return-stroke muscle (RSM) in the hippoid telson is a new muscle that is functionally and probably evolutionarily related to the uropod remoter muscle in the sixth abdominal segment, the latter being common to decapods with tailfans (Paul, 1981b; Paul et al., 1985). Thus, the appearance of the hippoid RSM may be an example of evolution of neuromusculature by division or duplication of ancestral neuromuscular elements (Antonsen and Paul, 2000). Since the actions of the return-stroke and remoter muscles are synergistic, uropod remotion, little central change may have occurred. The addition of the telson-uropod stretch receptors (Fig. 1, TUSRs), on the other hand, is expected to have necessitated adjustments in the sensory-motor circuitry in the terminal ganglion, and perhaps more anteriorly. The replacement of the spiking TUSR by a nonspiking TUSR in the evolution of the Hippidae, discussed above, is surprising. Does it mean that seniority plays a role in neural evolution? Neurons "recently" added to neuronal circuits could be more expendable than more ancient members of circuits, because they are not as highly interconnected, something which may happen gradually over time. This would restrain the rate at which structural changes in neuronal networks appear over evolutionary time.

Other neural characters besides those included in Fig. 1 confer evolutionary flexibility on neurobehavioural networks. In particular, the complexity and subtlety of neuromodulatory actions at many central and peripheral levels is only beginning to be understood (Katz and Harris-Warrick, 1999; Panksepp and Huber, 2002). The potential for change at discrete loci in a neuromodulatory system to dramatically alter a species behavior is exemplified by the loss in *M. quadrispina* of "the will" but not "the means" to fight conspecifics (Antonsen and Paul (1997). The diverse behaviours, generally smaller number of neurons, and, in some cases, simplifications of circuitry clearly make anomurans valuable subjects for many kinds of neurobiological research. Comparative investigations of their nervous systems are beginning to reveal the multiple levels at which neural evolution occurs.

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