

# Turning Loss Into Opportunity: The Key Deletion of an Escape Circuit in Decapod Crustaceans

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## Key Words

Crayfish · Disaptation · Escape response · Giant neurons ·  
Key deletion · Lobster · Startle response

## Abstract

Decapod crustacean escape responses are adaptive behaviors whose neural bases are well understood. The escape circuit is composed of giant neurons. Lateral giant interneurons (LGs) respond to posterior stimuli by generating a somersaulting tailflip; medial giant interneurons (MGs) respond to anterior stimuli with a backwards tailflip. Both sets of interneurons connect to giant fast flexor motor neurons (MoGs). Most features of the escape circuit are thought to result from strong selective pressure to respond to stimuli in the shortest possible time. Despite the apparent advantages of the escape circuit, it has been lost in multiple taxa independently. Some losses of the escape circuit may be rare cases of disaptation, where organisms are less well adapted than related species (i.e., those with the escape circuit). The losses of the escape circuit might be key deletions that promoted the radiation of decapod crustaceans by increasing selection pressure for species to evolve new anti-predator strategies and removing constraints against change.

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## Escape Responses as a Model System for Evolution

The concept of a key innovation is well known in evolutionary literature [Liem, 1973; Hunter, 1998; Hulsey, 2006; Seehausen, 2006]. Key innovations are features that might be linked to the origin of higher taxa, high incidence of speciation and adaptive radiation, and by their presence induce or promote even more evolutionary change in a taxon [Hunter, 1998]. For example, changes to the pharyngeal jaw may have facilitated the phenomenal radiation of cichlids in African rift lakes by permitting the oral jaws to specialize in dealing with diverse foods [Liem, 1973].

The converse idea of a key deletion – a loss of a feature in a taxon that acts as a creative evolutionary force – is largely absent [Porter and Crandall, 2003]. The losses of giant neurons responsible for rapid escape responses are potential examples of key deletions that might have contributed to the diversity of decapod crustaceans.

Decapod crustacean escape responses are excellent models for understanding behavioral and neuronal evolution. First, escape responses have obvious survival value [Bennett, 1984; Herberholz et al., 2004], which generates testable adaptive hypotheses. Second, escape responses are generated by dedicated neural circuits, so it is far easier to assess their contributions to behavior and fitness than most neural systems which are usually multifunctional [Healy and Rowe, 2007]. Third, the neurons involved are ancient, predating the origin of decapods

about 350 million years ago [Schram et al., 1978; Silvey and Wilson, 1979], and thus these neurons are widespread among taxa. Fourth, decapod crustaceans are tremendously diverse in morphology and behavior, with a thousandfold difference in scale between the largest and smallest known species [Martin and Davis, 2001]. Finally, decapod nervous systems have proved to be generally conservative, allowing differences to be identified against a backdrop of overwhelming similarity [Wiens, 1989; Kavanau, 1990; Arbas et al., 1991; Katz and Tazaki, 1992; Wiens and Wolf, 1993; Strausfeld, 1998].

### Escape Responses and Their Neural Bases in Crayfish

Decapod crustacean escape responses are a textbook case of natural behaviors explained in mechanistic terms, and have generated fundamental discoveries in neurobiology [e.g., electrical synapses; Edwards et al., 1999; Krasne and Edwards, 2002]. The vast majority of research on decapod crustacean escape responses has been conducted on one species, the Louisiana red swamp crayfish (*Procambarus clarkii*). The escape response and neural circuit are highly conserved in adult astacideans, an infraorder of Reptantia that includes crayfish and clawed lobsters [Parastacidae: *Cherax destructor*, Cooke and Macmillan, 1985; Astacidae: *Pacifastacus leniusculus*, Heitler and Fraser, 1993; Nephropidae: *Homarus americanus*, Lang et al., 1977; *Nephrops norvegicus*, Newland and Neil, 1990]. There is variation in development of the escape circuit in astacideans, however [Jackson and Macmillan, 2000].

Crayfish escape responses take the form of tailflips: rapid and powerful abdominal flexions and extensions (fig. 1). Tailflipping appears to be a single behavior at first glance, but a closer analysis reveals it to be three behaviors that differ both in their kinematics and underpinning neural circuitry.

When a crayfish receives a sudden tactile stimulus to the abdomen [Wine and Krasne, 1972; Herberholz et al., 2004], the first three abdominal segments flex, which results in the crayfish jackknifing into the water in a stereotyped trajectory. The response latency is usually less than 10 ms [Wine and Krasne, 1972; Reichert et al., 1981; Reichert and Wine, 1983]. The abdominal flexion is followed by a reflexive extension [Reichert et al., 1981]. This somersaulting tailflip is triggered by the LG interneurons. The LGs are a bilateral pair of chained neurons [Johnson, 1924; Wiersma, 1947] connected by electrical synapses, such that each chain effectively acts as one neu-

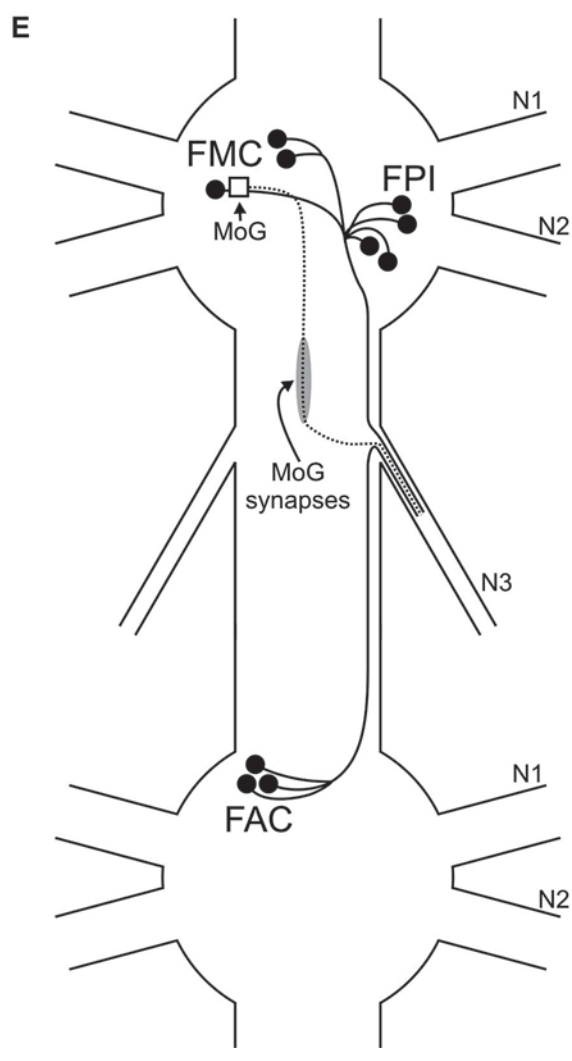
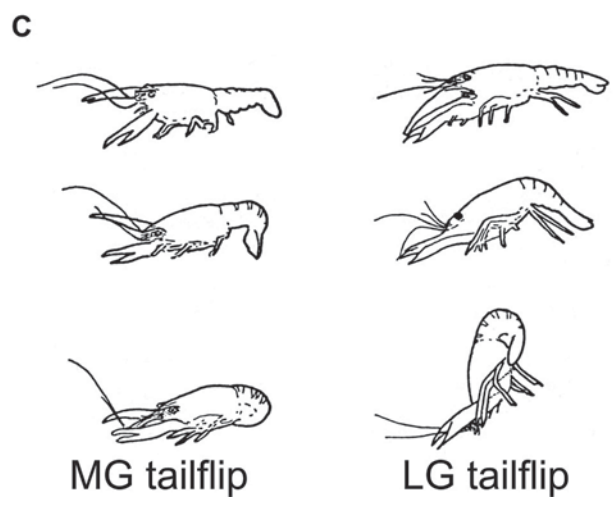
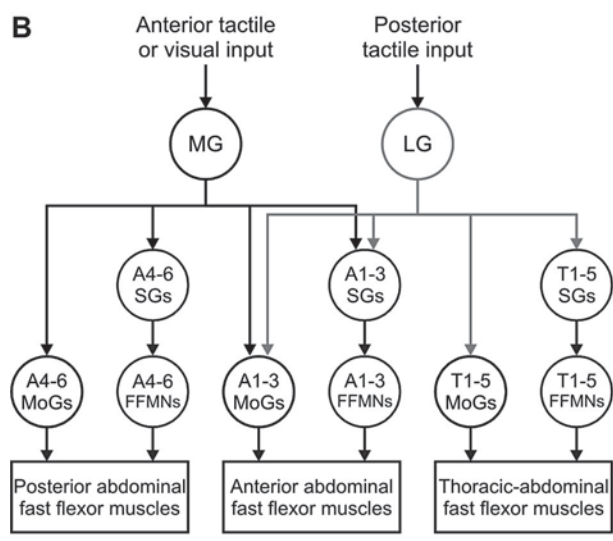
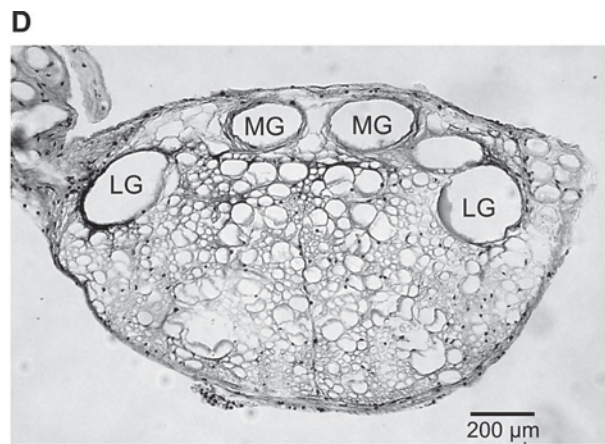
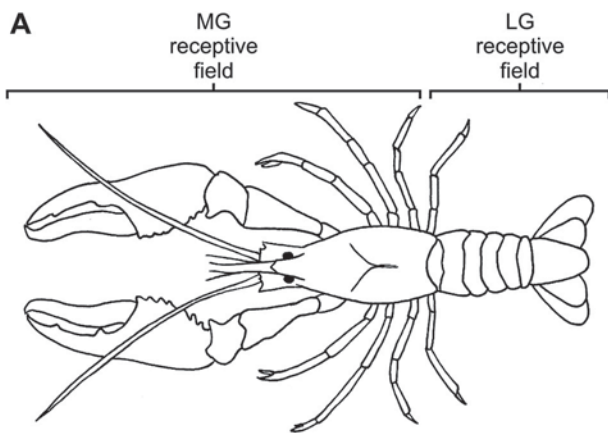
ron. This distinctive structure helps to identify homologues in other species: it is less plausible that a chain of giant neurons is due to convergence than a generic pair of giant neurons.

The kinematics of LG tailflips are largely explained by the pattern of synaptic connections made by the LGs with specialized fast flexor motor neurons, the motor giants (MoGs). The LGs synapse with the MoGs in the first three segments of the abdomen [Mittenthal and Wine, 1973] and the thorax [Heitler and Fraser, 1993]. The posterior three abdominal segments receive no input from the LGs when they fire, resulting in a somersaulting tailflip.

When a crayfish receives a sudden tactile stimulus to the head or thorax, or a sudden visual stimulus [Wine and Krasne, 1972; Herberholz et al., 2004], all the abdominal segments flex, causing the animal to move directly backwards in a stereotyped trajectory, away from the stimulus. These tailflips are triggered by medial giant interneurons (MGs), a bilateral pair of single neurons with the cell body located in the brain hemisegment contralateral to the main axon. Medial giant tailflips have a comparable latency to LG tailflips, and, like LG tailflips, are followed by a reflex extension. Unlike LGs, MGs synapse with MoGs in every abdominal segment [Mittenthal and Wine, 1973], but not the thoracic segments [Heitler and Fraser, 1993]. Thus, differing kinematics can be explained by the patterns of synaptic connectivity.

Early experiments implied that LGs and MGs caused tailflipping [Johnson, 1926; Wiersma, 1947], but it took almost fifty years to realize they are not active during repetitive tailflipping [Schrameck, 1970]. Giant neurons trigger only single tailflips [Wine and Krasne, 1972; Kramer and Krasne, 1984]. The neural basis of repetitive, non-giant tailflips is largely unknown, as these tailflips

**Fig. 1.** Escape circuit in crayfish (*Procambarus clarkii*). **A** External crayfish anatomy, showing spatial separation of input to giant neurons. **B** The core escape circuit that triggers abdominal flexion. Many known connections are omitted for clarity; see Wine [1984] for more detailed circuitry. **C** Form of escape tailflips based on Wine and Krasne [1972]. **D** Cross section of *P. clarkii* abdominal nerve cord, showing prominent dorsal axon profiles. **E** Location of the three clusters of fast flexor motor neurons cell bodies in abdominal ganglia based on Mittenthal and Wine [1978]. LG = Lateral giant interneuron; MG = medial giant interneuron; MoG = motor giant fast flexor motor neuron; SG = segmental giant interneuron; FFMNs = fast flexor motor neurons; T = thoracic ganglia; A = abdominal ganglia; FMC = flexor medial contralateral motor neuron cluster; FPI = flexor posterior ipsilateral motor neuron cluster; FAC = flexor anterior contralateral motor neuron cluster; N = nerve.



involve many non-giant neurons that are widely distributed throughout the nervous system [Reichert et al., 1981; Lee et al., 1995]. Non-giant tailflips can follow giant mediated tailflips [Reichert et al., 1981], be initiated voluntarily, or occur in response to predatory strikes when the giant interneurons do not fire [Herberholz et al., 2004]. Non-giant tailflips usually cause a crayfish to swim away from the source of a stimulus [Reichert and Wine, 1983].

Importantly, non-giant tailflips have significantly longer latencies than giant tailflips [Reichert et al., 1981; Reichert and Wine, 1983; Herberholz et al., 2004]. The escape circuit reduces response latencies by using giant neurons (which increase conduction velocity) and multiple electrical synapses (which minimize synaptic delay), which are hypothesized to be adaptations for generating short response latencies. Non-giant tailflips contribute to surviving predator attacks [Herberholz et al., 2004], but are not equivalent to giant mediated escape responses. Success at evading an initial predatory strike is about 50% for a giant tailflip, but only 20% for a non-giant tailflip [Herberholz et al., 2004]. Short latency escape responses should have survival value [Walker et al., 2005], so animals with only non-giant tailflips should be at a disadvantage compared to animals with both giant and non-giant tailflips.

At this level of analysis, crayfish escape behavior seems superbly elegant. An engineer starting from scratch might be hard pressed to create a more functional system. Different stimuli generate appropriately directed tailflips. Giant neurons and electrical synapses provide for short latency, but stereotyped responses. The non-giant circuit for repetitive tailflipping provides crayfish with flexibility and the potential for sustained escape. This picture is so intuitive and appealing that it was hypothesized that the escape circuit is widespread. 'Crustacea with a rapid tail flip can be expected to have giant fibers running the length of the cord' [Bullock and Horridge, 1965]. Neural circuits are not designed from scratch as an engineer would do, however, but are the products of tinkering with pre-existing historical circuits inherited from ancestral species. As more neurons in the escape circuit were studied, it became clear that engineering criteria failed to explain many aspects of the escape circuit [Krasne and Wine, 1984; Heitler and Fraser, 1986; Edwards et al., 1999].

Variation in neuron number is an example of a feature that is not readily predictable or explicable from engineering criteria. The fast extensor motor neurons are variable across crayfish species. There are six fast extensors per ganglion in *P. clarkii* [Wine and Hagiwara, 1977]

and *C. destructor* [Drummond and Macmillan, 1998], but eight in *P. leniusculus* [Leise et al., 1987]. These differences have no obvious functional consequences, because crustacean muscle fibers are often innervated by multiple motor neurons, whose innervation often overlaps substantially [Atwood, 1976].

The connection of the giant interneurons with the motor neurons of the fast flexor muscles (those responsible for generating tailflips) provides another example of unexpected features. The fast flexor muscles of each segment are innervated by about eleven fast flexor motor neurons (the number varies slightly from segment to segment in a single species): the MoG, about nine other excitatory non-giant motor neurons, and one inhibitory motor neuron [Selverston and Remler, 1972; Mittenthal and Wine, 1978]. These are located in three clusters (fig. 1e): the flexor medial contralateral (FMC) cluster, which contains the MoG and the inhibitor; the flexor posterior ipsilateral (FPI) cluster; and the flexor anterior contralateral (FAC) cluster [Mittenthal and Wine, 1978]. The MoGs are the only fast flexor motor neurons that receive monosynaptic input from the LGs and MGs via electrical synapses [Furshpan and Potter, 1957, 1959], and this is their only known input. The non-MoG fast flexor neurons are also excited by the giant interneurons, but not directly. The segmental giant interneurons (SGs) are interposed between the giant interneurons and the non-MoG fast flexor neurons [Roberts et al., 1982]. The SGs have a motor neuron-like morphology, but an axon entering the nerve leading to swimmerets ends before innervating any muscles [Fraser and Heitler, 1989]. The presence of the SGs was not suspected for years [Krasne and Wine, 1984]; they were difficult to detect due to the short synaptic delay, and there was no functional reason to expect them. The SGs are simple relays with no known integrative properties and add nothing to the motor pathway that a simple monosynaptic connection could not achieve. The SG neurons provide an example of how an evolutionary perspective might explain features that an engineering one does not. The motor neuron-like morphology of the SGs [Kramer et al., 1981] and the giant neurons' excitatory synapses with limb motor neurons [Cooke, 1985] prompted the hypothesis that the escape response originated as a limb-driven jump rather than a trunk-driven tailflip [Heitler and Darrig, 1986]. In this view, the SGs are 'a fossil in the layers of the circuit' [Edwards et al., 1999]. They were motor neurons innervating abdominal limbs, but lost their motor function as the escape response became increasingly powered by the abdomen over evolutionary time.



## The Early Evolution of the Escape Circuit

The behavior and neural anatomy of non-decapod crustaceans provides strong evidence that the escape circuit predates the origin of the decapods.

Stomatopods are distantly related to decapods (fig. 2), but may share one component in the escape circuit. The mantis shrimp species *Squilla mantis* may respond to anterior stimuli with variable, relatively long latency escape response that can involve limb-flicks, sometimes followed by abdominal flexion [Heitler et al., 2000]. The limb-flick behaviors are largely driven by a single pair of medial giant interneurons in the dorsal nerve cord. The name of these neurons is descriptive and was not selected to imply homology with crayfish, although homology might be assumed until evidence suggests otherwise [Brooks and McLennan, 1991]; figure 2 reflects a hypothesis of homology. These interneurons do not appear to drive abdominal flexion. There is no evidence for any precursor or homologue of the decapod LG system [Heitler et al., 2000]. Thus, mantis shrimp escape behavior generally supports the jump hypothesis.

Syncarids are thought to be the sister taxa to the decapods (fig. 2). The syncarid *Anaspides tasmaniae* has escape responses that are similar to tailflips, but because syncarids lack a carapace, the whole body, rather than just the abdomen, flexes and often rotates during escape responses [Silvey and Wilson, 1979]. *Anaspides tasmaniae* has LGs and MGs, and the anatomy of the LGs, as in decapods, consists of a segmented chain of giant neurons. Thus, the giant interneurons at the core of the escape circuit predate the origin of decapods. The earliest known decapod, *Paleopalaemon newberryi*, dates to the late Devonian [Schram et al., 1978], indicating that the escape circuit is over 350 million years old.

## The Pinnacle of the Escape Circuit

Most of the pelagic decapod crustaceans known as 'shrimps and prawns' belong to a paraphyletic group consisting of the decapod taxa Dendrobranchiata, Caridea, and Stenopodidia (fig. 2), but excluding Reptantia (primarily benthic crustaceans, such as lobsters and crabs). Shrimps and prawns arguably have the most sophisticated escape circuit, but their escape responses have been less well-studied than the reptantian escape responses [Arnott et al., 1998].

The LGs and MGs are myelinated in shrimps and prawns [Dendrobranchiata, Xu and Terakawa, 1999; Ca-

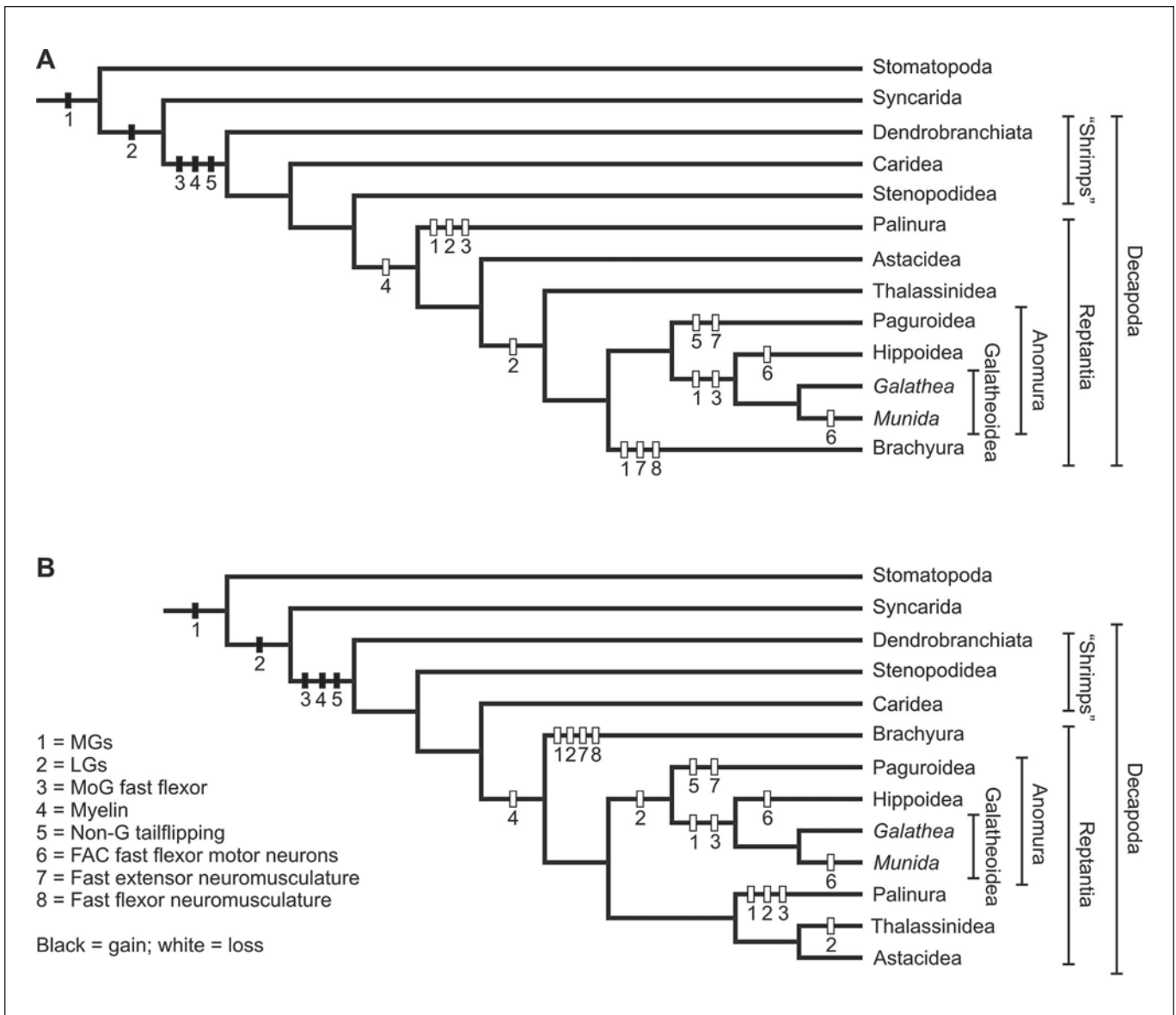
ridea, Stenopodidia, Holmes, 1942; Heuser and Doggenweiler, 1966]. The ultrastructure of decapod myelin differs from vertebrates', but the function of myelin is the same as in vertebrates, namely, that it increases conduction velocity. Indeed, the conduction velocities of the giant axons in several *Penaeus* species, 200 m s<sup>-1</sup>, are the fastest known in any animal [Xu and Terakawa, 1999]. The widespread phylogenetic distribution of this feature suggests that myelin originated once at the origin of the decapod clade. Myelin is arguably the only substantial innovation in the escape circuit after the origin of the decapods, and given that it should decrease response latency, myelin should be an adaptive feature that increases survival. Indeed, the high conduction velocity of shrimp led Ted Bullock to wonder, 'If nature can achieve these high velocities, why hasn't she used them more often in other groups? What are the costs?' [Bullock, 1984].

The left and right MoG axons are fused in all caridean shrimp species examined so far [Johnson, 1924; Holmes, 1942]. Such fusion should help synchronize contraction of the bilateral fast flexor muscles, and perhaps generate more powerful tailflips. Additionally, the MoG cell bodies have an unusual appearance in the dendrobranchiate shrimp species *Litopenaeus setiferus* [Faulkes, 2007], suggesting that there is yet more diversity in the escape circuit to be described in the non-reptantian decapods.

## The Dismantling of the Escape Circuit

The reptantian crustaceans include many of the familiar and commercially valuable decapods, including crayfish, lobsters, and crabs. This tremendous radiation of reptantian crustaceans is accompanied by a partial or complete dismantling of the putatively adaptive escape circuit (fig. 2). Two major hypotheses for reptantian phylogeny both require multiple independent losses of the escape circuit. Of five reptantian infraorders, Astacidea is the only one to retain the core escape circuit (LGs, MGs, and MoGs), and even they have lost some features seen in the non-reptantian shrimps and prawns. The giant interneurons are not myelinated in any reptantian species, which is surprising considering the hypothesis that there is high selection pressure for escape responses to be rapid. Likewise, the MoGs are not fused in any reptantian species [Wiersma, 1947].

The LGs, MGs, and MoGs have been lost in infraorder Palinura, which includes spiny lobsters (Palinura) [Espinoza et al., 2006] and slipper lobsters (Scyllaridae) [Faul-



**Fig. 2.** Two hypothesized phylogenies of taxa discussed in text, with characters of the escape circuit added. **A** Phylogeny based on Scholtz and Richter [1995] and Ahyong and O’Meally [2004]. In this scenario, the escape circuit was lost twice: once in *Palinura*, and a second time in the clade containing *Thalassinidea*, *Anomura*, and *Brachyura*. **B** Phylogeny based on Porter et al. [2005]. In this scenario, the escape circuit was lost on three separate occasions, and the LG neurons were lost in a fourth event.

kes, 2004]. The loss in spiny lobsters is particularly unexpected as they were predicted to have the escape circuit due to their overall similarity to clawed lobsters in morphology, behavior, and life history [Faulkes, 2004], unlike the more highly modified scyllarids. The loss of the escape circuit seems to be correlated with new anti-predator strategies in palinurans; e.g., heavy armor and spines

[Barshaw et al., 2003], powerful and sustained non-giant tailflipping [Jacklyn and Ritz, 1986; Jones, 1988; Spanier et al., 1991], and concealment by digging [Faulkes, 2006].

Infraorder *Thalassinidea* (ghost shrimp and mud shrimp) have lost the LGs. The MGs, though smaller than crayfish MGs [*Callinassa californiensis*, Turner, 1950],

appear to function in escape responses, as suggested by the presence of MoGs [*Upogebia pugettensis*, Paul et al., 1985]. The loss of LGs has been hypothesized to be correlated with burrowing and ‘backing away from danger’ [Paul, 1989]. Given the complexity and diversity of burrow structure [Nickell and Atkinson, 1995; Bird and Poore, 1999], however, it is not clear why the MGs, but not the LGs, should be retained. Mud shrimps can tailflip repeatedly, presumably using non-giant tailflipping. Little else is known about their tailflipping behavior or the anatomy or physiology of the MGs.

Members of the infraorder Anomura lack LGs, but few other generalizations can be made about the diverse escape circuits in this taxon [Paul, 2003].

Asymmetric hermit crabs (superfamily Paguroidea) have multiple changes in the escape circuit that are correlated with living in vacated snail shells. As in thalassinid mud shrimp, hermit crabs have MGs [Chapple, 1966; Chapple and Hearney, 1976] and MoGs [Umbach and Lang, 1981], but not LGs [Wiersma, 1961; Chapple and Hearney, 1976]. The MGs still cause an escape response, but this is a rapid withdrawal into a shell, rather than a tailflip [Chapple, 1966; Umbach and Lang, 1981]. As in crayfish, SGs are interposed between MGs and fast flexor motor neurons [Heitler and Fraser, 1986, 1987]. The initial escape flexion cannot be followed by an extension (as in crayfish) because the entire fast extensor musculature, including the motor neurons, has been lost [Chapple and Hearney, 1976]. There is no equivalent behavior to non-giant tailflipping. Many aspects of the escape circuit are asymmetric in the hermit crabs that have been examined. For example, there are six fast flexor motor neurons on the right, but only four on the left in *Pagurus pollicarus* [Chapple, 1969]. The size of the MG axons in *P. pollicarus* is also asymmetrical, with the right MG larger than the left [Chapple and Hearney, 1976]. Further, the MGs can fire separately in *P. granosimanus* [Chapple, 1966], unlike the obligate coupling in crayfish and lobster [Wiersma and Turner, 1950; Lang and Govind, 1978]. These asymmetries do not prevent hermit crabs from occupying shells that spiral in the opposite direction, however [MacGinitie, 1937].

The abdominal neuromusculature of several interesting taxa allied to commonly known asymmetric hermit crabs has not been examined, including symmetrical hermit crabs (family Pylochelidae) and the king crabs (family Lithodidae). The lithodids are of particular interest because they have frequently been thought to be derived from more typical hermit crabs [McLaughlin, 1983; Cunningham et al., 1992; Richter and Scholtz, 1994;

McLaughlin and Lemaitre, 1997; Morrison et al., 2002], although a more recent analysis links lithodids to hippid sand crabs [McLaughlin et al., 2007]. Lithodids have greatly reduced abdomens and tend to be more symmetric, and as such are excellent candidates to show additional modifications, most probably deletions, of the escape circuit. Indeed, examining the escape circuit might help clarify their relationship with other anomurans.

All other anomurans examined have lost the MGs, LGs, and, with one possible exception, the MoGs. Two squat lobster species (superfamily Galatheoidea) have been examined in detail, and the composition of their fast flexor motor neurons differs substantially. The FAC fast flexor motor neuron cluster is present in *Galathea strigosa* but not *Munida quadrispina*. In *G. strigosa*, none of the neurons in the FMC cluster of fast flexor motor neurons have the anatomical specializations of the MoG, but a large, unspecialized fast flexor excitor sits in the approximate location that the MoG does in other species [Sillar and Heitler, 1985], which is hypothesized to be a MoG homologue. There is no equivalent cell in *M. quadrispina* [Wilson and Paul, 1987], nor in any other species without the escape circuit. At a minimum, the presence of this hypothesized MoG homologue in only one species indicates that outright deletion of the MoGs is more common than the MoG ‘joining the pack’ of fast flexor motor neurons. Going further, the presence of the MoG homologue in only one species suggests an alternative hypothesis, namely that this neuron in *G. strigosa* is not homologous to the MoG, but is rather a new neuron, perhaps generated by an extra division of a motor neuron stem cell during development. This hypothesis is consistent with the variable number of fast flexor and extensor motor neurons across species.

Sand crabs (superfamily Hippoidea) also lack LGs, MGs, MoG [Paul et al., 1985], and the fast flexor motor neuron FAC cluster [Paul, 1989]. Non-giant tailflipping is used in digging in sand crabs [Faulkes and Paul, 1997], and undergoes substantial modification in hippid sand crabs, becoming limb-driven uropod beating [Paul et al., 1985; Paul, 1989, 1990, 1991, 2003].

The so-called ‘true’ crabs in infraorder Brachyura are recognized, in part, by the almost or complete absence of a large, flexible tail, so it is extremely unlikely that they have any trace of the escape circuit [Wiersma, 1961]. Some crabs have large axons in the dorsal portion of the nerve cord [Skobe and Nunnemacher, 1970; Fraser, 1974], but there is no evidence that these are homologues to MGs and LGs.

## Loss as a Creative Evolutionary Force

Despite the prediction that the retention of escape circuits should be subject to extreme positive selection pressure [Bennett, 1984], losses predominate. Two prominent hypotheses for the relationships of reptantian decapods both indicate multiple, independent losses of the escape circuit (fig. 2). These losses are not confined to relic taxa ('nooks and crannies'), but are widespread among successful taxa. Using 1,614 North American decapod species [Williams et al., 1988] as a representative sample of the proportions of crustacean taxa worldwide, 31.5% of those species are predicted to have a complete escape circuit with myelin, 18.7% are predicted to have a non-myelinated escape circuit, 13.1% are expected to have MGs, but not LGs, only, while 36.6% of species have lost the escape circuit entirely, most of which are brachyuran crabs. Brachyuran crabs are a fantastically successful group by any measure, but spiny lobsters, squat lobsters, sand crabs, and so on are hardly rare. Thus, the loss of the escape circuit is a candidate example of a key deletion.

Why was the ostensibly adaptive decapod escape circuit not maintained? Plausible adaptive scenarios can be constructed for some features: hermit crabs living in snail shells would probably gain no survival value from the fast extensor musculature, or from LG neurons that respond to sudden stimuli on the abdomen. Other losses are more difficult to explain, such as the complete loss of the escape circuit in palinurans. Palinurans' defensive capabilities (e.g., spines, armor) might compensate for the absence of a short-latency, giant-mediated escape response [Barshaw et al., 2003]. Nevertheless, the morphology of palinurans does not preclude rapid escape tailflips; on the contrary, powerful and sustained non-giant tailflipping is an important part of their behavioral repertoire [Spanier et al., 1991]. Given this, an animal with armor and rapid escape responses would seem to have an advantage over one with armor alone.

Another hypothesis for why the escape circuit was not maintained is that there was a trade-off. For example, the large amount of space giant neurons occupy could be replaced with many smaller neurons, which could increase the available 'computational power,' and perhaps result in greater behavioral flexibility or complexity. A 'back of the envelope' calculation indicates that one giant axon of 200  $\mu\text{m}$  diameter, which is near the maximum diameter for MG and LG [Wine and Krasne, 1972] uses the same space as about 177 axons with a somewhat large diameter of 15  $\mu\text{m}$ . This is a substantial value given that an abdominal ganglion contains only about 650 cell bodies [Wine,

1984]. There is no evidence that species without giant neurons have made such a trade-off, however.

With no current adaptive hypothesis to explain the losses of the escape circuit, an alternative hypothesis is that some losses of the escape circuit are disaptations: features that have demonstrably lower survival value than those of ancestral taxa [Baum and Larson, 1991]. The disaptation hypothesis predicts that slower escape responses result in lower survival, and that tailflips by spiny lobster are significantly slower than giant-mediated tailflips in clawed lobsters, for example. Disaptations are rare, but putative examples exist in nature [Montgomery and Clements, 2000; Sidell and O'Brien, 2006]. That disaptations are rare would not stop them from having major long-term consequences once established. Disaptations might be tolerated under conditions of low competition or relaxed selective pressure [Montgomery and Clements, 2000]. Spiny lobsters, for example, are thought to have originated in the deep ocean [George and Main, 1967] and ancestral palinurans might have lived in similar conditions. A deep ocean habitat may have provided refuge from predators and been a sufficiently lenient environment for the loss of the escape circuit to become fixed. As palinurans extended into shallower, warmer waters, they might have experienced greater predation, thus facing increased selective pressure favoring either new anti-predator strategies or elaborating on existing ones [Espinoza et al., 2006], as re-evolving the escape circuit is unlikely. The sub-optimal condition (i.e., lacking a fast escape response) would become an impetus for later evolutionary innovations. The scenario is generally similar to a taxon that has sub-optimal features due to environmental change: environmental change pushes it off an adaptive peak and must climb back up, perhaps to several new and different adaptive peaks. Here, the cause of the poorly adapted condition is internal (e.g., loss of adaptive neural circuit) rather than external (e.g., changing environment).

Losses of the escape circuit might also have facilitated evolutionary innovation by reducing constraints that would have prevented modifications of the abdomen [Paul, 2003]. Interactions between neurons and muscles during development might provide a mechanism whereby escape-related neurons could constrain change in their downstream targets. Neural activity can influence muscle development in crustaceans [Mellon and Stephens, 1978; Atwood and Lnenicka, 1987] and conversely, muscle fiber growth influences neural synapses [Lnenicka and Mellon, 1983]. The loss of the escape circuit might have facilitated reduction in overall size of the abdomen



[an aspect of carcinization, McLaughlin and Lemaitre, 1997], as large fast flexor muscles that power the fast tail-flip are expected to be maintained if the escape circuit is present. This is clearly not a necessary relationship, however, as palinurans maintain large muscles and powerful tailflips despite the absence of the escape circuit.

Many changes in the escape circuit are probably selectively neutral. Variation in the number of non-giant fast flexor motor neurons, including the complete deletion of some clusters, has no clear correlation with any behavioral change [Wilson and Paul, 1987]. Such changes, however, leave species with significantly different evolutionary potential [Paul, 2003], in that they have different substrates on which evolutionary forces (selection, drift, etc.) might act.

Originally, research on the escape circuit was used to shed light on behavior; now, more behavioral research is required to shed light on the escape circuit, and particularly the hypothesis that the loss of escape responses is a key deletion. For species such as shrimps, prawns, and mud shrimp, many aspects of escape behavior are either unknown [e.g., kinematics, response latency, receptive fields] or are not easily explained by what is known from crayfish escape responses [e.g., how body roll is achieved in some shrimps, Arnott et al., 1999]. There are also little data quantifying the survival value of fast escape responses during real interactions with predators, although research on crayfish provides a valuable starting point [Herberholz et al., 2004].

Surveying the basic neuroanatomy of a wider breadth of species would provide clearer understanding of evolutionary trends versus happenstance. The variation between the squat lobster *G. strigosa* and *M. quadrispina* highlights the risks of using one species to represent

whole families or infraorders. The possibility of discovering new configurations of the escape circuit, even in well-studied species, is highlighted by the recent recognition of the loss of the escape circuit in palinurans [Faulkes, 2004; Espinoza et al., 2006]. This could have been established decades ago, but Wiersma missed an opportunity when he wrote that the MGs and LGs in scyllarid lobsters were 'not at all conspicuous' rather than concluding they were absent [Wiersma, 1961]. Given the ease of identifying the neurons involved, describing the main neurons in the escape circuit for many species is very feasible.

Darwin famously wrote, 'It may be said that natural selection is daily and hourly scrutinising, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good...' [Darwin, 1859]. The decapod crustacean escape circuit provides an example suggesting that natural selection's scrutiny is not perfect. Fortunately, if the loss of an adaptive feature is not immediately fatal, loss might be followed by innovation. In crustaceans, such innovations include the increased use of weaponry (e.g., spiny lobsters), armor, whether by thickening the exoskeleton (e.g., slipper lobsters) or using discarded shells (e.g., hermit crabs), or concealment by burrowing (e.g., as in mud shrimp and sand crabs). In this way, loss of an adaptive system might be a springboard to new heights rather than consignment to a dead end.

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