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Review Paper

New evidence on an old question: Is the "fight or flight" stage present in the cardiac and respiratory regulation of decapod crustaceans?

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ABSTRACT

The ability to stay alert to subtle changes in the environment and to freeze, fight or flight in the presence of predators requires integrating sensory information as well as triggering motor output to target tissues, both of which are associated with the autonomic nervous system. These reactions, which are commonly related to vertebrates, are the fundamental physiological responses that allow an animal to survive danger. The circulatory activity in vertebrates changes in opposite phases. The stage where circulatory activity is high is termed the "fight or flight stage", while the stage where circulatory activity slows down is termed the "rest and digest stage". It may be assumed that highly evolved invertebrates possess a comparable response system as they also require rapid cardiovascular and respiratory regulation to be primed when necessary. However, in invertebrates, the body plan may have developed such a system very differently. Since this topic is insufficiently studied, it is necessary to extend studies for a comparative analysis. In the present review, we use our own experimental results obtained in the crab *Neohelice granulata* and both older and newer findings obtained by other authors in decapod crustaceans as well as in other invertebrates, to compare the pattern of change in circulatory activity, especially in the "fight or flight" stage. We conclude that the main features of neuroautonomic regulation of the cardiac function were already present early in evolution, at least in highly evolved invertebrates, although conspicuous differences are also evident.

Contents

Abbreviations: ANS, autonomic nervous system; CG, cardiac ganglion; CIR, cardioinhibitory response; DA, dopamine; GABA, gamma-aminobutyric acid; GABAi, GABA-like immunoreactivity; HR, heart rate; 5-HT, 5-hydroxytryptamine (serotonin); IHR, instant heart rate; IHR_M, mean IHR; OA, octopamine; PSNS, parasympathetic nervous system; PTX, picrotoxin; RCA, reversible cardiac arrest; SNS, sympathetic nervous system; SEG, subesophageal ganglion; VDS, visual danger stimulus; VR, ventilation rate..

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1. Introduction

Regulation of physiological activities in animals is crucial for the preservation of homeostasis (Cannon, 1932). Such activities include the acceleration and deceleration of the heart rate (HR) in response to different behavioral and physiological requirements. In vertebrates, this physiological regulation is mediated by a part of the peripheral nervous system named the autonomic nervous system (ANS). This system is the primary mechanism of control of the "fight or flight" response and its role is mediated by two different components that reside in the spinal cord: the sympathetic nervous system (SNS) and the parasympathetic nervous system (PSNS). These two systems have opposite effects on the activity of organs. Normally, excitation of the SNS increases the HR by means of epinephrine and norepinephrine, whereas excitation of the PSNS decreases the HR by means of acetylcholine. The SNS prevailing situation, with high HR and low digestive movements, is termed the "fight or flight" stage. This stage describes the behavior of animals that either fight against or flee from enemy or danger. In contrast, the PSNS overriding situation, with a high level of digestive movements and a low HR, is termed the "rest and digest" stage (Cannon, 1929, 1932; Shimizu and Okabe, 2007).

A third subdivision of the ANS, often described as "intrinsic" or "enteric" because it was studied mainly in the digestive tract, is also termed "metasympathetic" (Nozdrachev, 1983). This system includes neural elements located inside the internal organs, whose main function is not to modulate but to trigger their activity. The SNS and PSNS exert their influence on the vital functions of the body through these intrinsic neural elements (Shuranova et al., 2006).

In fishes, the ANS has an architecture (Nieuwenhuys et al., 1998) similar to that of mammals, suggesting that the ANS originated in vertebrates (Sarnat and Netsky, 2002). In contrast, decapod crustaceans have no structural counterpart of the ANS. Thus, an intriguing question is how cardiac and respiratory regulation is achieved in these animals. Could there be a "functional counterpart" or a totally different type of mechanism is involved?

Decapods are easily involved in agonistic encounters where the "fight or flight" stage has been observed. However, a cardiac alternate response before either a neutral sudden stimulus or a menacing stimulus is a prominent feature which is also present in other invertebrate and vertebrate phyla. In the present review, we use our own experimental results in the crab *Neohelice granulata* and both older and newer findings obtained by other authors in other decapod crustaceans to describe the patterns of change in circulatory activity against environmental disturbances and in anticipation of a social interaction. We also discuss up to what point the functional basis of the ANS can be generalized in decapod crustaceans.

2. The "fight or flight" stage

Crustaceans, particularly crayfishes and lobsters, have been widely used as models to study aggression because they frequently get involved in aggressive and submissive behaviors (Dingle, 1983; Hyatt, 1983; Kravitz and Huber, 2003; Rutishauser et al., 2004). The involvement in agonistic behavior is a necessary condition to examine the physiological regulation of the "fight or flight" responses. Cuadras (1980, 1981) early established that the HR of hermit crabs is affected during agonistic interactions. Later, (Li et al., 2000) investigated the blind cave crayfish *Orconectes australis packardi* Rhoades to establish whether it altered its HR during social interactions. To this end, these authors paired isolated crayfish and allowed them to interact while monitoring their HR. It became clear that various types of contacts could result in different alterations in the HR. For example, the more physical the interaction (such as a pushing match with chelae), the higher the HR. The smallest changes occurred during non-physical contact interactions and the HR increased significantly from baseline levels during four behavioral acts (walking, antennae touch, tailflip/retreat, pushing battle) (Li et al., 2000).

Although the above-mentioned authors did not assess alterations in the ventilation rate (VR), other authors (Wilkens, 1976; McMahon and Wilkens, 1983) had examined this parameter previously. These authors demonstrated that the VR represents a functional state that correlates to environmental changes (light flashes, movements in the crab's visual field, water currents, brushing mechanoreceptors), thus indicating that, like HR, the VR allows assessing the degree of homeostatic perturbation (autonomic state) in the animal. Schapker et al. (2002) assessed both the HR and the VR together in the crayfish *Procambarus clarkii* to study the function of this autonomic state both before and during agonistic encounters. These authors tested the hypothesis that when two crayfish saw each other and visually displayed postural signals, which indicated a pending aggressive encounter, some physiological processes, such as an increase in the ventilation and cardiac performance, would prepare the animal for the potential body and cellular stress. They demonstrated that upon anticipation of a social interaction with another crayfish, both HR and VR increased. During an agonistic encounter between two crayfish, the level of HR and VR correlated with the intensity of the interaction. The authors concluded that such rapid responses in the cardiac and respiratory systems suggested an autonomic-like regulation associated with the "fight or flight" stage (Schapker et al., 2002).

HR was monitored in lobsters before, during and after agonistic encounters between two animals housed together in a confined space to establish whether the cardiac frequency relates in any direct way to social status (Hernandez-Falcon et al., 2005). The authors concluded that, by far, the largest effect observed was a correlation of the HR and the contest outcome. That is, winners exhibited increases in the HR that were greater and lasted longer periods of time than those of losers. They also found that both animals showed increases in cardiac frequency as fights progressed, but that the ultimate winner showed larger increases. Moreover, the HR of the winning animal was maintained at a higher level for at least 15 min after the end of the fight, constituting a long-term component.

Our own recent data also suggest that the HR in the crab *Neohelice* increases during agonistic interactions (Canero E.M., unpublished observations).

The fact that decapod crustaceans show the "fight or flight" type of response during social interactions supports the idea of an autonomic-like reflexive control of cardiac function.

3. The "alternate response"

Although it is well accepted that animals increase their VR and cardiac output after sudden stimuli (Wingfield, 2003), many animals across different taxonomic groups such as mollusks (Wells, 1980; Wells et al., 1987; King and Adamo, 2006), crustaceans (Cuadras, 1980), fish (Axelsson et al., 1987), amphibians (Laming and Austin, 1981), birds (Cohen and Macdonald, 1971), and mammals (Smith et al., 1981), show an alternate response to sudden environmental stimuli of different modalities. The alternate response includes a decrease in the VR, a decrease in the cardiac output and an interruption of the heart rhythm, inducing reversible cardiac arrest (RCA) (Cuadras, 1981). Behaviorally, the alternate response is accompanied by an orientation response (Shuranova and Burmistrov, 1996), a startle response (Grober,