Aggression in invertebrates

Edward A Kravitz* and Robert Huber†

Invertebrates are outstanding model systems for the study of aggression. Recent advances and promising new research approaches are bringing investigators closer to the goal of integrating behavioral findings with those from other disciplines of the neurosciences. The presence of highly structured, easily evoked behavioral systems offer unique opportunities to quantify the aggressive state of individuals, to explore the mechanisms underlying the formation and maintenance of dominance relationships, to investigate the dynamic properties of hierarchy formation, and to explore the significance of neural, neurochemical and genetic mechanisms in these behavioral phenomena.

Addresses
*Department of Neurobiology, Harvard Medical School, 220 Longwood Avenue, Boston, MA 02115, USA
e-mail: edward_kravitz@hms.harvard.edu
†Bowling Green State University, Biological Sciences, Life Sciences Building, Bowling Green, OH 43403, USA
e-mail: lobsterman@caspar.bgsu.edu

Current Opinion in Neurobiology 2003, **13**:736–743

This review comes from a themed issue on
Neurobiology of behaviour
Edited by Mark Konishi and Randolf Menzel

0959-4388/$ – see front matter

DOI 10.1016/j.conb.2003.10.003

Introduction

This review describes several invertebrate models in which intraspecific aggression is readily evoked in dyadic interactions between animals; these models enable studies to be performed at levels ranging from the behavioral through the physiological and ultimately to the molecular and genetic levels. Elegant models of interspecific aggression in invertebrates also exist [1], but these will not be dealt with here. In the species described here, agonistic behavior patterns appear to be pre-wired in the nervous system, as animals with no previous social experience can engage conspecifics in normal agonistic encounters. During such fights, paired animals exchange highly stereotypical behaviors that escalate through different intensity levels and that, ultimately, result in a decision with behavioral consequences for both winners and losers. A common theme in these studies is that amines, peptides and steroid hormones, substances that function as neuromodulators and/or as neurohormones, serve as important modulators of aggression.

Aggression in social insects: bees, ants, wasps and termites

It may be surprising that aggression is seen in social insects, considering that selfish behavior is rare in groups with shared reproductive interests, such as honey bee colonies; however, stereotyped agonistic behavior within a hive [2] is common during worker policing [3,4]. Moreover, aggression in the context of nestmate recognition has been explored in ants [5,6], bees [7], wasps [8] and termites [9] where the determination of self versus non-self is frequently based on the expression of cuticular hydrocarbon profiles [10,11]. With pheromonal commands reflecting the collective needs of the colony [12], many aspects of social behavior are under endocrine and genetic control, including the reproductive division of labor [13–15•], investments in reproductive individuals [16], drone assassinations, queen execution by workers [17,18] or queen duels [19]. As in many other systems, agonistic success is fostered by physical superiority [20], promotes reproductive opportunities [21] and correlates with amine function [22].

Aggression in other invertebrates: spiders and dragon flies

Ritualized displays and cues that are predictive of agonistic success enable the assessment of a rival's relative fighting ability, in particular, in species with dangerous weapons, such as spiders [23]; the strategies that underlie aggression and intraspecific, intersexual cannibalism in this group [24–26] are shaped by the structure of the population [27]. Dominance enhances feeding opportunities in dragon flies [28] but few physiological studies that relate specifically to aggression have been carried out using these models.

Aggression in non-social insects: crickets

Detailed electrophysiological studies have been carried out in crickets, particularly looking into acoustic signaling. (Singing is used in mating behavior and in aggression in crickets and other insects [29].) Amine neuron systems (serotonin, octopamine, dopamine and histamine) have been fully mapped in cricket nervous systems, including those systems present in the brain and the ventral nerve cord (reviewed in [30]). Depletion of nervous system amines, either globally using reserpine or selectively with blockers of synthesis specific for serotonin or for octopamine/dopamine, produces alterations in aggression, but these effects are subtle [31]. Although reserpine depletes the nervous system of all amines and produces lethargic behavior, crickets are able to fight at different levels of intensity. Selective depletion of serotonin had no effects on fighting behavior, whereas octopamine/dopamine depletion lowered the intensity of fights. The authors conclude that octopamine and/or dopamine are not required for the function of motor circuits involved in aggression, but that they do seem to play a role in releasing the behavior in response to appropriate stimuli. Other studies report that brain levels of serotonin are lowered in losing males during fights, but only if the wings that are important in singing behavior are intact [32]. Removal of the wings results in lowering of brain serotonin in both winners and losers of fights. Injections of the opioid antagonist naloxone enhanced aggression in losing male crickets and in females [33], while injection of a vertebrate μ-opioid agonist reduced aggression in male winners. These results suggest that status-specific effects must be considered when injecting drugs into winning and losing animals for this kind of study. Interestingly, it has been demonstrated that forcing losing male crickets to fly after agonistic encounters rapidly restores their willingness to fight [34]. This fact, well known to gamblers involved in cricket-fighting, requires an intact ventral nerve cord between the brain and the thoracic segments of the nerve cord.

Crustacean models of aggression

The first anatomical and physiological studies with crustacean species were performed more than 100 years ago. Indeed, the eminent figures TH Huxley, S Freud and G Retzius conducted extensive early anatomical studies on the nervous systems of these organisms. In the mid-twentieth century, fundamental questions of synaptic physiology were answered by B Katz, SW Kuffler, P Fatt, CAG Wiersma and others, due to the anatomical simplicity of their peripheral nervous systems of the crustacean models. These same systems now provide exciting information on neuronal function at a 'systems' level; thus, important studies with the crustacean stomatogastric ganglion describe, at the level of identified neurons, how modulation affects the output of a neural network [35]. A more recent frontier in which, once again, crustacean models offer opportunities that are not readily available with other species, is in the study of social behavior. Crustaceans such as crayfish and lobsters appear to be ideal for exploration of the neural basis of aggression because: (1) their structurally elegant, modular neural systems feature relatively few, large aminergic neurons, whose distribution has been mapped and whose physiological properties have been defined [36•,37••]; (2) the behaviorally relevant neural circuits have also been mapped [38•–40] and socially modulated changes in these circuits that relate to amine neuron function can be observed [39,41••]; (3) amine levels can be both monitored [42] and experimentally altered [43–46]; (4) stereotyped behavioral acts can be represented by quantitative measures in many contexts [47] and finally; (5) crustacean individuals maintain a fundamentally solitary existence, with dominance resulting largely from physical superiority. By contrast, fighting success in other systems is often determined by an ability to form coalitions or by differential treatment of kin.

Agonistic meetings between crayfish or lobsters in controlled laboratory situations feature a series of highly structured behavioral acts, with escalation being governed by strict rules. Fights progress through ritualized visual displays, antennae whipping, claw lock, wrestling and, if physical asymmetries are only minor, brief periods of unbridled claw use [48–50]. The expression of particular fighting strategies varies with hunger states [51], body size [52] and previous agonistic success [53]. Although fighting frequently serves to obtain or defend resources, such as shelter [54] or mates [55], its occurrence, particularly in the absence of a resource, suggests an inherent predisposition towards agonism [56,57].

As in other groups, amine neuron systems (serotonin and octopamine) are implicated as key physiological regulators of agonistic behavior and social dominance in crustaceans [37••,42], but controversy surrounds the experimental results in this area and their interpretation by different authors. Acute, experimental injections of serotonin and octopamine in lobsters (*Homarus americanus*) produced postures resembling those seen in dominant (serotonin-like posture) and subordinate (octopamine-like posture) animals during and after agonistic encounters [58]. It was these observations that inspired the detailed examination of the roles of amines in aggression in crustaceans by many authors, using a variety of species. Postural changes and enhancement of aggression were recently reported in a second lobster species (*Munida quadrispina*) [59]. Acute and constant infusion of serotonin in crayfish (*Astacus astacus*) produces aggression with a unique specificity: after a delay of 10–30 min, treated individuals engage larger opponents in prolonged bouts of fighting, even in instances that carry substantial risk of injury [46,50,60•–62]. Conversely, in a different species of crayfish (*Procambarus clarkii*), serotonin injections produced postural changes that did not resemble those seen during agonistic encounters; serotonin injections also reduced levels of aggression in agonistic encounters, whereas a serotonin analogue enhanced aggression [43]. In interpreting these observations, other authors do not focus on a direct role for serotonin in decapod aggression; instead, they suggest that serotonin treatment in *H. americanus* might indirectly affect social interactions through an inhibition of retreat in the losing animals [63]. Crayfish with lowered serotonin levels (*Orconectes rusticus*) are indistinguishable from controls in terms of fighting behavior [45], but serotonin-depleted lobsters showed enhanced levels of aggression [44], similar to those initially reported when serotonin levels were raised in lobsters and crayfish [60•]. One interpretation of such apparently contradictory results focuses on the possibility that levels of serotonin within a narrow window of concentration might have to be released at the correct time and place in the nervous