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A behavioral analysis of force-controlled operant tasks in American lobster

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ABSTRACT

Operant conditioning is a common tool for studying cognitive aspects of brain functions. As the first step toward understanding those functions in simple invertebrate microbrains, we tested whether operant conditioning could be applied to train American lobster *Homarus americanus* that has been extensively adopted as an animal model for neurophysiological analyses of nervous system functions and behavioral control. The animal was trained by food rewarding for gripping of a sensor bar as the operant behavior. Lobsters were first reinforced when they acted on the bar with a stronger grip than a pre-set value. After this reinforcement, the animal learnt to grip the bar for food pellets. The yoked control experiment in which the animal received action-independent reinforcement excluded the possibility of pseudoconditioning that the food simply drove the animal to frequent gripping of the sensor bar. The association of the bar-grip with food was extinguished by rewarding nothing to the operant behavior, and was restored by repeating the reinforcement process as before. In addition, lobsters successfully carried out differential reinforcement regarding the gripping force: their gripping force changed depending on the increased force threshold for food reward. These data demonstrate that lobsters can be trained by operant conditioning paradigms involving acquisition and extinction procedures with the precise claw gripping even under the force control.

1. Introduction

Operant conditioning is one of the most common tools for the studies of animal learning and cognition [1–3]. In cognitive neuroscience, mammals and avian species have been mainly used as experimental animals and various manipulative operant tasks (lever-press or key-peck) have been developed for them [4–6]. Recent research using operant paradigms, however, has shown that some invertebrates with a “microbrain” [7] or a “mini-brain” [8] that is characterized by not only its size but also its cytoarchitecture and neuronal organization also possess cognitive abilities [9,10] including simple forms of rule learning or concept formation [11], count [12] and observational learning [13]. Physiological mechanisms underlying these higher-order functions of the microbrain, however, remain to be clarified because of experimental difficulties in most cases.

American lobster *Homarus americanus* has major three advantages for neurophysiological analysis of brain functions. First, the animal can perform a precise limb movement that is recommended as an operant target in most learning experiments [14,15]. The lobster has a pair of asymmetrical claws as the first thoracic appendages: the crusher is a stout, molar-toothed, slow-acting claw while the cutter is a slender, incisor-toothed, fast-acting claw. The former type is usually used for breaking clamshell by gripping (defined by [16]) to eat shellfish meat so that its action can be precisely controlled regarding the direction of movements and the grip force [17]. Second, the lobster nervous system is easily accessible for neurophysiological analysis. Decapod crustaceans, such as lobsters, crayfish, and crabs, have been used for many researches on sensory and motor functions at the level of identifiable neurons and neuronal networks [18]. This characteristic of the nervous system can be also useful to analyze mechanisms underlying brain functions in crustaceans. Finally, crustaceans including lobsters and crayfish are phylogenetically close to insects that were demonstrated to show a variety of cognitive brain functions. Recent studies on phyletic evolution of arthropods have revealed that crustacean is quite likely an ancestral lineage of hexapoda [19–22], suggesting that some primitive forms of cognitive brain function can be found in crustaceans. In particular, it is noteworthy that anatomical similarity of brain structure between crustaceans and insects also indicates their phyletic relationship [23].

As the first step toward understanding the higher-order brain function in lobsters, basic operant procedures were conducted in the present study to associate manipulative task with food as the reward. Since lobsters can perform precise gripping actions by chelipeds [15,24,25], we utilized them as an operant target. For this purpose, we developed an operant chamber for lever-press type conditioning. This system allowed the animals to perform free operant reward learning.

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The pressure sensor system in the chamber quantitatively measured the gripping force of lobsters. Using this quantitative measurement system, we also analyzed whether lobster could carry out differential reinforcement procedures on the grip force. The results demonstrated the applicability of the bar-grip paradigm in lobsters for studying their learning ability and higher-order brain functions.

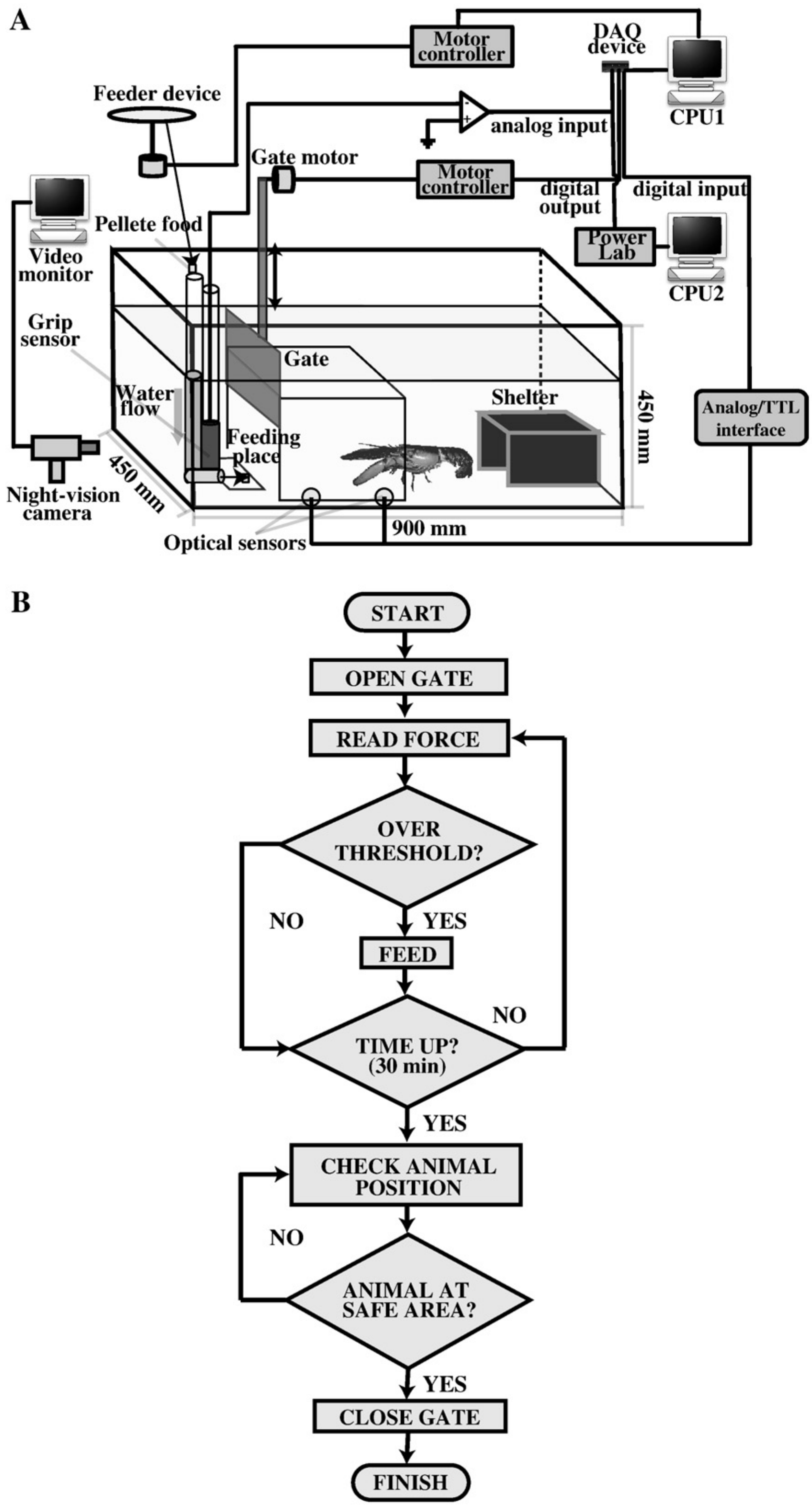

Fig. 1. Experimental set-ups. A: Operant chamber system adopted in the present study. Bar-gripping was detected by a load sensor whose output was fed into CPU1 that controlled the feeder system and the gate for feeding place depending on the griping force. The sensor signal was also fed into CPU2 for continuous recording throughout the experiment. B: Flowchart of the training program. All of the possible actions and responses by the subject during training were presupposed and appropriately dealt with in the program by continuously monitoring the animal behavior throughout two pairs of optical sensors as well as a grip sensor.