Neuroscience and Biobehavioral Reviews 35 (2011) 474–482

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Review

What's on the mind of a jellyfish? A review of behavioural observations on *Aurelia* sp. jellyfish

David J. Albert

Roscoe Bay Marine Biology Laboratory, 4534 W 3rd Avenue, Vancouver, British Columbia, Canada V6R 1N2

ARTICLE INFO

Article history:
Received 14 March 2010
Received in revised form 30 May 2010
Accepted 3 June 2010

Keywords:
Aurelia sp
Behaviour
Nervous system
Sensory receptors
Scyphozoa

ABSTRACT

Aurelia sp. (scyphozoa; Moon Jellies) are one of the most common and widely distributed species of jellyfish. Their behaviours include swimming up in response to somatosensory stimulation, swimming down in response to low salinity, diving in response to turbulence, avoiding rock walls, forming aggregations, and horizontal directional swimming. These are not simple reflexes. They are species typical behaviours involving sequences of movements that are adjusted in response to the requirements of the situation and that require sensory feedback during their execution. They require the existence of specialized sensory receptors. The central nervous system of *Aurelia* sp. coordinates motor responses with sensory feedback, maintains a response long after the eliciting stimulus has disappeared, changes behaviour in response to sensory input from specialized receptors or from patterns of sensory input, organizes somatosensory input in a way that allows stimulus input from many parts of the body to elicit a similar response, and coordinates responding when stimuli are tending to elicit more than one response. While entirely different from that of most animals, the nervous system of *Aurelia* sp. includes a brain that creates numerous adaptive behaviours that are critical to the survival of these phylogenetically ancient species.

Contents

E-mail address: djalbert@interchange.ubc.ca.

0149-7634/$ – see front matter
doi:10.1016/j.neubiorev.2010.06.001

1. Introduction

To the casual observer, jellyfish seem to do little more than drift lazily and swim slowly. The absence of the familiar bilaterally symmetrical nervous system with its large aggregation of neurons in the head creates the perception that jellyfish have no brain (Gehring, 2001) and leads to the expectation that their organized behaviour will be minimal. From this perspective, the answer to the question posed in the title is simple: nothing can go on in the mind of a jellyfish because it doesn't even have a brain! Its behaviour very likely consists of a few simple reflexes.

Jellyfish have thrived where millions of other species have perished. The adaptations of these 500 million year old species are so successful that they now seriously impact human activity. Jellyfish consume huge amounts of larvae of fish targeted for human consumption (Arai, 1988; Bailey and Batty, 1984a,b; Cowan and Houde, 1993; Moller, 1984; Purcell et al., 1994; Purcell and Arai, 2001; Southward, 1955), and they consume crustaceans and other marine life that might otherwise be food for commercially important fish stocks (Arai, 1988; Bailey and Batty, 1984a,b; Moller, 1984; Purcell and Arai, 2001). The proliferation and spread of jellyfish in recent years has enhanced the visibility of their impact on commercial fishing (Hay et al., 1990; Russell, 1970) and other human activities (Burnett, 1991; Heeger et al., 1992; Matsueda, 1969). This is all quite remarkable for species that are vulnerable to predation and lacking in protective covering.

Aurelia sp. (Moon Jellies) are members of the phylum Cnidaria, considered to be the oldest multiorgan phylum of animals. They belong to the scyphozoan class of jellyfish and are one of the most common, most widely dispersed, and most studied jellyfish in the world's oceans. Three morphologically distinct species are recognized (*Aurelia labiata*, *Aurelia aurita*, and *Aurelia lambata*) but there are several times as many populations that are genetically different enough to qualify as distinct species (Dawson, 2003; Dawson and Jacobs, 2001; Gershwin, 2001; Schroth et al., 2002). There are no known behavioural differences between these species. In the remainder of this paper I will use the term *A. aurita* or *A. labiata*, when the species observed is known and the term *Aurelia* sp. when the species is uncertain.

The nervous system of a jellyfish is organized very differently from that of other animals. Their central nervous system is a group of nerve nets and bundles around the inner margin of the bell (Anderson, 2004; Mackie, 2004; Satterlie, 2002). An appreciation of the functional effectiveness of this central nervous system and its contribution to the survival of these species requires a systematic examination and understanding of their behaviours. This paper will review behavioural studies of *Aurelia* sp. jellyfish. The term 'mind' in the title is used in a colloquial sense to indicate that I will take issue with the common notion that jellyfish do not have a brain like other animals and, therefore, cannot have a substantial behavioural repertoire. This review will demonstrate that the preponderance of *Aurelia* sp. behaviours are not simple reflexes but species typical behaviours that are flexible in their execution and guided by sensory feedback. Far from being slow, these behaviours can occur within seconds of the effective stimulus.

In *Aurelia* sp., eight sensory centers, rhopalia, are equally spaced around the margin of the bell. They contain what appear to be light receptors (ocelli) and gravity sensors (statocysts). Chemosensors and mechanoreceptors are spread over most of the medusa's exterior surface. These sensory systems appear to send input to the central nervous system around the inner margin of the bell (Mackie, 2004; Singla and Weber, 1982).

Aurelia sp. are primarily carnivores. A distinguishing feature of *Aurelia* sp. and all other cnidarians is that they have nematocysts. Nematocysts are organelles within cnidocytes. They are launched outward from the medusa's surface when touched. There are many different types of nematocysts but two main types appear involved in predation (Kass-Simon and Scappaticci, 2002; Peach and Pitt, 2005): (1) nematocysts that penetrate the skin of the prey and inject a toxin, and (2) nematocysts that become wrapped around a struggling prey. The poison kills small crustaceans or larvae within minutes. Larvae that touch the medusa's surface may release 100 or more nematocysts (Heeger and Moller, 1987). *Aurelia* sp. have nematocysts on the exumbrella (exterior surface of the bell), along the tentacles, and on the oral arms (Southward, 1955).

I will begin this review by describing the stimuli that *Aurelia* sp. can detect. I will then review the evidence on how *Aurelia* sp. respond to various stimuli. Because of the limited amount of research available on *Aurelia* sp., I will consider evidence from other cnidarians and other invertebrates when it seems appropriate. Finally, I will categorize the way *Aurelia* sp. respond to stimuli in order to infer processes that may occur in their central nervous system.

2. Sensory capacities

2.1. Light receptors

Aurelia sp. are sensitive to light. For example, horizontal directional swimming was observed in Saanich Inlet only on days when it was sunny (Hamner et al., 1994). What is not certain is the location of the photoreceptors. Each of the eight rhopalia on the bell margin has two ocelli that have the appearance of being photoreceptors. Extracellular electrophysiological recordings from ocelli find changes in electrical activity associated with light stimuli in the hydrozoan jellyfish *Polyorchis penicillatus* and *Sarsia tubulosa* (Weber, 1982a,b). The apical ends of what appear to be photoreceptors contain opsin proteins (Martin, 2002). Axons from the ocelli go into the outer nerve ring (Singla and Weber, 1982). The spectral sensitivity of the extracellular electrical responses in the ocelli of some hydrozoan jellyfish are similar to what have been found recently in the cubozoan jellyfish, *Tripedalia cystophora*, that have image forming eyes (Coates et al., 2006). The opsin proteins in the photoreceptors of cnidarians are similar from one species to another (Gehring, 2001; Martin, 2002). The accumulating evidence suggests that the ocelli of *Aurelia* sp. are the photoreceptors that are responsible for their light sensitivity.

2.2. Mechanoreceptors

Aurelia sp. are responsive to touch. They increased their swimming speed after being touched on the side of the bell with tentacles of the gelatinous predators *Phacellophora camtschatica* or *Cyanea capillata* (Hansson and Kultima, 1996; Strand and Hamner, 1988). Touch by tentacles of *C. capillata* or a piece of string also caused *Aurelia* sp. to swim up (Hansson (1997).

The receptors responsible for somatosensory sensitivity are uncertain. Cnidocytes in a variety of cnidarians, including