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

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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.

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doi:10.1016/j.neubiorev.2010.06.001

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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 anemones, hydrozoans, and scyphozoans, contain mechanoreceptors that along with chemoreceptors modulate the sensitivity of nematocysts. This modulation serves to both sensitize and desensitize the nematocysts to optimize their effectiveness (Oliver et al., 2008; Purcell and Anderson, 1995; Thurm et al., 2004; Watson and Hessinger, 1994). There are neural connections between cnidocytes (Oliver et al., 2008; Thurm et al., 2004). Cnidocytes and their associated mechanoreceptors are distributed over most of the surface of *Aurelia* sp. as is somatosensory sensitivity (Albert, 2008; Hansson, 1997; Hansson and Kultima, 1996). Accordingly, it seems reasonable to suggest that the mechanoreceptors associated with the cnidocytes of *Aurelia* sp. send axons into the central nervous system and subserve a somatosensory function (Singla, 1983).

2.3. Chemoreceptors

Like mechanoreceptors, chemoreceptors are associated with cnidocytes. These chemoreceptors are extraordinarily sensitive and can detect the chemical scent of an organism as it swims past (Watson and Hessinger, 1994). They also respond to chemicals released when prey are wounded by nematocysts (Watson and Hessinger, 1994). The demonstrated function of these chemoreceptors is to modulate the discharge of nematocysts (Oliver et al., 2008; Purcell and Anderson, 1995; Thurm et al., 2004; Watson and Hessinger, 1994). The mechanoreceptors and chemoreceptors are neurally connected (Oliver et al., 2008; Thurm et al., 2004). It seems reasonable to suppose that the cnidocytes on *Aurelia* sp. have chemoreceptors and that these chemoreceptors have neural connections to the central nervous system.

There are also chemoreceptors in the lateral tracts of the oral arms. Their demonstrated function is to limit the captured objects that enter the gastric cavity to those that have a chemical signature of protein. Captured material that does not appear to be protein is discarded back into the water from the oral arm (Archdale and Anraku, 2005; Southward, 1955).

Aurelia sp. are inferred to have salinity sensors since they avoid areas with salinity less than about 20 ppt (parts per thousand; Albert, 2008; Han and Uye, 2009; Lo and Chen, 2008; Mutlu, 2001; however, see Russell, 1970 for observations in the Baltic Sea). There is no evidence on the location of salinity sensors. Since *Aurelia* sp. also avoid parts of the water column with low oxygen content (Hamner et al., 1982; Papathanassiou et al., 1987; Mutlu, 2001), it seems reasonable to infer that they also have oxygen sensors or receptors sensitive to chemicals that correlate with dissolved oxygen.

2.4. Gravity sensors

The eight rhopalia around the bell margin have a calcium sulfate statolith and a touch plate lined with cilia. The change in position of the statolith with the orientation of the medusa alters the stimulation of cilia on the touch plate. This stimulation allows a medusa to orient with respect to gravity (Arai, 1997; Horridge, 1969; Mackie, 1980).

2.5. Sound pressure wave and vibration sensors

Sensitivity to sound pressure waves and vibration has been inferred from behavioural observations. One of these observations is that *A. labiata* stayed below turbulent water (Albert, 2007). It was inferred that the stimulus for this behaviour was vibration or sound pressure waves from the turbulent water above them. Ciliary hairs in the statocysts of prawns, squid, and octopi are sensitive to sound pressure waves (Hu et al., 2009; Lovell et al., 2005, 2006). Ciliary hairs may be directionally sensitive (Corwin, 1981; Fay et al., 1974; Horridge, 1969; Singla, 1975). Mechanoreceptors associated with cnidocytes may also subserve vibration and sound pressure wave sensitivity (see Section 2.2 above).

Field observations have also been made on the distance sensing of two pseudothecosomatous pteropods, *Gelba cordata* (Forskal) and *Corolla spectabilis* (Dall). These planktonic opisthobranch gastropods were able to sense a diver from 1 m away as indicated by the execution of escape diving in response to the diver's approach (Gilmer, 1972). Sensitivity to sound pressure waves in these species is presumably mediated by ciliary hairs.

2.6. Directional sensor

Aurelia sp. swam to the southeast repeatedly over a 2-month period in Saanich Inlet (Hamner et al. (1994). Directional swimming was activated by sunlight but the stimulus controlling the actual direction of swimming was not determined. There was no indication that the medusae were orienting to tidal current or wave direction. The sensory basis for this behaviour is unknown.

2.7. Hydrostatic pressure receptor

Aurelia sp. sometimes accumulate at specific depths. For example, in Saanich Inlet they were present down to about 30 m (Hamner et al., 1994). In Mljet Lake, medusae were distributed from about 5 to 20 m deep during the day but were below 25 m at night (Malej et al., 2007). *Aurelia* sp. tended to occur in shallow coastal areas during the spring and summer but were found by trawl fishermen in deep water during the winter (Russell, 1970).

While it seems reasonable to suggest that *Aurelia* sp. may change their position in the water column as the location of prey change, Lo and Chen (2008) and Hamner et al. (1982) have not found that aggregations of *Aurelia* sp. follow either the horizontal or the vertical location of prey closely. Whether *Aurelia* sp. can use depth as a guiding stimulus has not been thoroughly investigated. They may have a depth sensing mechanism (Rice, 1964). Hair cells of the statocysts respond to hydrostatic pressure in numerous invertebrate species (Fraser, 2006; Fraser et al., 2003).

The scyphozoan *Periphylla periphylla* normally resides in deep water (200 m). These medusae migrate to within 50 m of the surface at night (Kaartveld et al., 2007). Hydrostatic pressure could be the guiding stimulus for these migrations. *Chrysaora hysoscella* (scyphozoa) have also been observed positioning themselves at particular depths in the water column (Hays et al., 2008).

2.8. Summary

Aurelia sp. have receptors that respond to light, touch, gravity, chemicals, sound pressure waves, direction, vibration, and hydrostatic pressure. Knowledge of these sensory systems is uneven. Little is known about the way sensory systems connect to the central nervous system around the bell margin.

3. *Aurelia* sp. behaviours

Sensory systems of *Aurelia* sp. provide the central nervous system with a stream of sensory input about the environment. The central nervous system in turn generates behaviours that protect medusae from harm and enable them to forage and reproduce successfully. In the material that follows, I will review the behaviours displayed by *Aurelia* sp.

3.1. Diel vertical migration

Migration to deep water during the day and to surface layers at night is a common behaviour in zooplankton that helps them avoid predation. While a laboratory study by Mackie et al. (1981)

has frequently been cited as evidence that *Aurelia* sp. display diel vertical migration (Arai, 1997; Graham et al., 2001; Hamner, 1995), field observations do not support that conclusion. In Urazoko Bay (Yasuda, 1973), Elefsis Bay (Papathanassiou et al., 1987), the Black Sea (Mutlu, 2001), and Mljet Lakes (Malej et al., 2007), medusae were deepest in the water column at night, the reverse of the pattern associated with diel migration. In most other locations, medusae were present throughout the water column at most hours during the day, except for the top 2 m (Albert, in press; Graham et al., 2001; Han and Uye, 2009; Lo and Chen, 2008; Papathanassiou et al., 1987; Toyokawa et al., 1997; Yasuda, 1973). In the late afternoon or early evening, *Aurelia* sp. sometimes moved into the surface layer and remained there for several hours but not for the entire dark period (Albert, 2005, in press; Hamner et al., 1994; Papathanassiou et al., 1987).

3.2. *Response to somatosensory stimulation*

Stationary *Aurelia* sp. swam rapidly away when touched by a tentacle of the predatory jellyfish *P. camtschatica* (Strand and Hamner, 1988) and increased their pulse rate and swam up when touched by tentacles of the predatory scyphozoan *C. capillata* (Hansson, 1997; Hansson and Kultima, 1996). In more recent observations, *A. labiata* swam upward for at least 1 m when touched by a soft, hollow, silicone rubber ball, a soft, spherical sponge, or an oyster shell (Albert, 2008). Upward swimming was elicited even when the touch stimulus consisted of placing a silicone ball or foam sponge against the manubrium and simply rotating it 90° (Albert, 2008). In contrast, *Aurelia* sp. did not swim upward following touch by a conspecific (Albert, 2008; Hansson, 1997; Hansson and Kultima, 1996).

Following somatosensory stimulation, *A. labiata* turned and arrived at a vertical trajectory quickly and without directional searching (Albert, 2008; Hansson, 1997). While the touch stimulus lasted for only 1 or 2 s, upward swimming continued for at least 30 s or 1 min in these two experiments (Albert, 2008; Hansson, 1997) or until the medusa reached the surface (Albert, 2008). Vertical swim speeds were 1–1.5 m/min (Albert, 2008; Hansson, 1997).

3.3. *Response to low salinity*

In Tapong Bay (Taiwan), *Aurelia* sp. disappeared from some areas when salinity dropped below 20 ppt (Lo and Chen, 2008). Mutlu (2001) and Han and Uye (2009) observed some medusae in salinity of 18–20 ppt. In Roscoe Bay, British Columbia, *A. labiata* avoided surface water with a salinity of less than 20 ppt (Albert, 2008).

Chrysaora quinquecirrha, another scyphozoan, tolerated salinity down to 13 ppt in the estuary of Chesapeake Bay (Feigenbaum and Kelly, 1984). In a laboratory study, the hydrozoan, *S. tubulosa*, and the ctenophore, *Pleurobrachia pilus*, inhabited water with salinity down to 10 ppt (Arai, 1976).

3.4. *Response to turbulence*

Aurelia sp. regularly swam down and below the turbulent water when they were swept over a gravel bar on ebb tides in Roscoe Bay (Albert, 2007, 2009). Medusae accumulated below the ebb stream in water that was still or in a counter current that moved them back toward the gravel bar. When occasionally a medusa swam up into the moving water, it was buffeted by the ebb stream and swam back down. When the ebb ended, medusae swam up into the still water and drifted back into the bay on the nonturbulent flood tide (Albert, 2007).

The interpretation of these results was that medusae dove in response to being tumbled by the turbulent water (Albert, 2007). Once in still water, they sensed sound pressure waves or vibration created by the turbulent ebb stream and remained below the ebb stream until that stimulation disappeared. An alternative explanation is that medusae dove as well as remained below the ebb stream because of sound pressure waves and vibration.

3.5. *Distance sensing*

Dense aggregations of *A. labiata* always formed several meters from the rock walls in Saanich Inlet (Hamner, et al., 1994) and Roscoe Bay (Albert, 2008). While a few medusae could be seen within one meter of a rock wall, by far the greatest number stayed several meters away. These observations suggest that *Aurelia* sp. have a distance sensing ability. Sensitivity to sound pressure waves appears to be the only known sensory system that might participate in distance sensing.

Medusae were almost never stranded by ebb tides in Roscoe Bay (Albert, 2009). On an ebb tide, most medusae were in the top half of the water column in shallow areas and drifted out of the shallow area while the water was still more than 2 m deep. When the depth of the water column was about 1 m, the few medusae still in shallow water occasionally swam down and bumped into rocks on the bottom (Albert, 2009). Their response to this collision was to swim upward, usually to the surface. When they were at the surface, medusae were in the moving water of the ebb stream and drifted toward deeper water. Because the diving behaviour only happened when the depth of the water column reached about 1 m, it seemed that medusae must have a distance sensing mechanism that gave them information about their proximity to the bottom.

Pelagia noctiluca (scyphozoa) also appears to have a distance sensing ability that helps them avoid stranding. When they were near a windward shore, *P. noctiluca* dove in the water column but stayed about 0.5 m above the bottom by active swimming (Zavodnik, 1987).

3.6. *Foraging*

Aurelia sp. captured most prey on the exumbrella or tentacles (Bailey and Batty, 1983; Heeger and Moller, 1987; Southward, 1955). From the exumbrella, ciliary currents moved prey to food pouches in the marginal groove. Tentacles with prey attached contracted and prey were transferred to the marginal groove. Prey were licked off the marginal groove by the oral arms and carried centripetally by ciliary currents in the lateral tract of the oral arm. Ciliary currents moved captured items that did not have a chemical signature associated with protein out of the lateral groove and they were eventually released back into the water (Archdale and Anraku, 2005; Henschel, 1935, cited by Southward, 1955; Southward, 1955). Captured items that were recognized as containing proteins were transported in the lateral groove of the oral arm to the oralgastular canal by ciliary hairs (Archdale and Anraku, 2005; Henschel, 1935, cited in Southward, 1955; Southward, 1955).

Stimulation of chemoreceptors on the oral arm by captured prey had a major impact on subsequent foraging. Bailey and Batty (1983) recorded a 4-min swimming tract of *A. aurita* in a glass container (30 × 10 × 22 cm) filled only with seawater. Each medusa was then allowed to capture a single *Clupea harengus* larva (Atlantic herring larva) and move it onto the oral arm. After larva capture, swimming speed increased and the pattern changed from one of swimming primarily at the surface or bottom of the tank to one of swimming through the entire tank. The faster swimming speed made it easier for the tentacles to capture additional prey by increasing the speed of eddy currents at the bell margin (Costello and Colin, 1994, 1995). Swimming speed did not continue to increase as more larvae were captured and actually decreased when 5 or 6 larvae had been captured.

Increased swimming speed after prey capture has also been observed in the scyphozoan *C. quinquecirrha* (Ford et al., 1997; Matanoski et al., 2001). The ctenophore *Beroe cucumis* increased its swimming activity following exposure to water conditioned by its prey, *Bolinopsis infundibulum*, or by homogenate of *B. infundibulum* (Swanberg, 1974; Falkenhaug and Stabell, 1996).

There are no demonstrations that *Aurelia* sp. are able to navigate toward prey. Hamner and Schneider (1986) suggested that *Aurelia* sp. accumulated at the convergence of Langmuir Cells in the Berring Sea because they were attracted to prey (amphipods) that accumulated there. However, Larson (1992) argued that *Linuche unguiculata* (scyphozoa) accumulated in Langmuir Cells in the Carribean as a result of lateral advection and upward swimming. No objective observations were provided to support either of these conjectures. More *P. camtschatica* were present in areas of Saanich Inlet where its prey (*Aurelia* sp) were in dense aggregations (Strand and Hamner, 1988). However, *P. camtschatica* may have encountered the aggregations of *Aurelia* sp. by chance and remained there because of their foraging success.

Contrary to the argument that *Aurelia* sp. navigate toward prey, the location of *Aurelia* sp. in Tapong Lagoon (Taiwan) was negatively correlated with the location of prey (Lo and Chen, 2008). The negative correlation may reflect the foraging success of the *Aurelia* sp. aggregation and the failure of the aggregation to move once most prey at one location had been captured.

Only one set of controlled observations has evaluated whether *Aurelia* sp. are attracted to the scent of prey. Arai (1991) observed the response of 24-h food-deprived *Aurelia* sp. to dissolved chemicals associated with prey in a 70 l enclosure. Water flowed into the tank from each end and drained at the middle in such a way that there was little mixing of fluid from the two sides. The filtered seawater flowing into one side had recently contained *Artemia* nauplii (brine shrimp). Filtered sterile seawater flowed into the other side. Individual, 24-h food-deprived *Aurelia* sp. spent about 80% of a 30-min observation period in the side of the apparatus containing water conditioned with A*rtemia* nauplii. Medusae did not swim toward the source of prey-related chemicals (Arai, 1991). In another location, *Aurelia* sp. captured yolk-sac herring or capelin larvae but did not swim toward larvae (Oiestad, 1985; Details of the observations are not provided.).

It is worth noting that the molluscs *Aplysia juliana* and *Aplysia californica*, that also rely on the use of chemosensors, both display an ability to navigate toward food (see also, Ferner and Weissburg, 2005; Webster and Weissburg, 2009). *A. juliana* that had buried themselves in the sand, almost immediately climbed out of the sand when their preferred food, sea lettuce (*Ulva lactuca*), was placed in their aquarium (Frings and Frings, 1965). If the water circulation pumps were turned off, *A. juliana* would navigate directly to the food. *A. californica* were observed in a Y-maze. When food was placed in one arm, they navigated into the arm with food on 90% of the trials. When the tentacles containing their chemosensors were removed, 70% of the test animals did not move into either arm (Audesirk, 1975).

3.7. Horizontal directional swimming

Horizontal directional swimming by *Aurelia* sp. has been documented most thoroughly by Hamner et al. (1994) in Saanich Inlet. Medusae swam to the southeast on numerous days during July and August. Directional swimming occurred when it was sunny but not when it was cloudy. Hamner et al. (1994) imply that directional swimming occurred predictably on sunny days but no quantitative evidence was presented on its regularity. They do describe individual instances where medusae that were swimming directionally in sunshine, stopped doing so when cloud cover formed. These observations suggest that sunlight elicited the swimming to the southeast but they do not isolate the stimulus guiding the direction of swimming. Individual episodes of directional swimming were sustained for 15–20 min. During July, large numbers of medusae were at the north end of Saanich Inlet but by September, there were few in the north and large aggregations in the south.

Directional swimming by *A. labiata* occurred occasionally in Roscoe Bay but was not a regular occurrence (Albert, 2008). Aggregations of *Aurelia* sp. have been observed swimming in a uniform direction in Monterey Bay (Graham et al., 2001). However, there were no systematic observations.

Directional swimming by the scyphozoan *Mastigias* has been thoroughly documented for several lakes in Palau (Dawson and Hamner, 2003; Hamner and Hauri, 1981). *Mastigias* regularly swam from one end of a lake to the other in the morning and then swam back in the afternoon. In some instances, the daily swimming served to keep the symbiotic zooxanthellae that accompany *Mastigias* in the sunlight so as to perpetuate photosynthesis. Several lakes in Palau have *Mastigias* and the direction of swimming was different for each lake. When *Mastigias* from one lake were placed in another, they displayed the swimming direction of their lake of origin (Hamner and Hauri, 1981). Hamner and Hauri (1981) suggest that medusae were using the angle of incidence of sunlight to guide the directional swimming, but there are no supporting observations.

The scyphozoan *Stomolophus meleagris* L. Agassiz displayed directional horizontal swimming over 15–20 min at Cape Lookout, North Carolina (Shanks and Graham, 1987). It was unclear whether the medusae were using wave orientation, tidal currents, or some other cue to maintain their swimming orientation. Medusae whose orientation was altered by experimentally created turbulence, eventually resumed their original swimming orientation.

When *S. meleagris* were tumbled by waves or bumped the bottom as they neared the shore, they reportedly turned and swam in a direction 180° from their previous direction of swimming (Shanks and Graham, 1987). No quantitative data were accumulated to substantiate these observations.

The stimuli guiding directional swimming by *Aurelia* sp., *Mastigias*, and *S. meleagris* are unknown.

3.8. Aggregation and spacing behaviour

Aurelia sp. are frequently in dense aggregations in coastal water (Hamner et al., 1994; Toyokawa et al., 1997; Purcell et al., 2000; Magome et al., 2007). Aggregation also occurs in lagoons and semi-enclosed small bays where the effects of tides, winds, and currents are greatly diminished. In Tapong Bay (Taiwan) most *Aurelia* sp. accumulated at the southeast end of the lagoon, the part of the lagoon farthest from the tidal entrance (Lo and Chen, 2008). Medusae location was negatively correlated with the location of prey and uncorrelated with chlorophyll, temperature, or salinity. In Honjo District (a lagoon off Nakaumi Lake near Tokyo Bay), *Aurelia* sp. accumulated in three aggregations rather than being evenly dispersed across the lagoon. Two years prior to this study, medusae had formed a single aggregation in the center of the lagoon (Han and Uye, 2009, p. 812). In Roscoe Bay, *A. labiata* were dispersed across the entire bay over a 2-year period when the population was large but usually accumulated in a single group at the west end of the bay over a 2-year period when the population was small (Albert, 2009). These observations suggest that *Aurelia* sp. exert some control over their horizontal distribution. *Aurelia* sp. and other cnidarians may also exert some control over their geographic location along entire coastlines (Doyle et al., 2007; Hay et al., 1990; Sparks et al., 2001).

Hamner et al. (1994) have made the only observations that give a clue as to how the dense aggregations of *Aurelia* sp. form. When solitary medusae swam toward an aggregation (see above, Section

3.7), they were swimming horizontally. After encountering a group of conspecifics, they changed to vertical swimming. In this way, they were recruited into the aggregation. No numerical data were presented to establish the consistency of this behaviour or to specify how close to conspecifics a horizontal swimming medusae came before changing its swimming pattern from horizontal to vertical. Recruitment into aggregations following horizontal swimming has not been reported elsewhere (Albert, 2009; Purcell et al., 2000). Solitary *Aurelia* sp. in Saanich Inlet swimming at a large distance from dense aggregations were reported to be physically damaged (Hamner et al., 1994).

Aurelia sp. space themselves vertically. They were spread through large parts of the water column in Elefsis Bay (Greece, Papathanassiou et al., 1987), Tokyo Bay (Toyokawa et al., 1997), Honjo District, Nakaumi Lake (Han and Uye, 2009), and Roscoe Bay (Albert, in press). The exception was that the top 2 m of the water column contained few medusae during the day. In Elefsis Bay (Papathanassiou et al., 1987), Saanich Inlet (Hamner et al., 1994) and Roscoe Bay (Albert, 2005), medusae frequently entered the top 2 m of the water column in the late afternoon or early evening and continued to occupy that zone for several hours.

The scyphozoans *S. meleagris*, *P. noctiluca*, *Mastigias*, and *L. unguiculata* also form dense aggregations (Hamner and Hauri, 1981; Larson, 1992; Malej, 1989; Shanks and Graham, 1987).

3.9. Swimming in a vertical circle

In Prince William Sound (Alaska, Purcell et al., 2000) and Theodosia Inlet (British Columbia, Strand, 2003), dense aggregations of *Aurelia* sp. sometimes swam in a vertical circle. Medusae at one end of the aggregation swam up, and those at the other end swam down. These formations were several meters in diameter. The frequency of occurrence and duration of this swimming pattern has not been explored. This pattern of aggregation has not been reported for other cnidarians.

Purcell et al. (2000) speculated that medusae swimming in vertical circles were following convection currents created by wind or current shear. However, the vertical circular swim pattern in Theodosia Inlet, British Columbia was observed in a sheltered bay with only enough wind to create a ripple on the water (Strand, 2003).

3.10. Tidal vertical migration

Migration into surface water during a rising tide and to the bottom of the water column during a falling tide is used by some zooplankton to maintain their location in an estuary or to move higher into an estuary (Schwamborn et al., 2008; Trinast, 1975; Wooldridge and Erasmus, 1980). By staying in surface water during a rising tide, zooplankton drift further into an estuary along with the inward moving tidal water. Conversely, by staying close to the bottom during an ebb tide, zooplankton stay in a portion of the water column that moves least during the ebb tide.

Van der Veer and Oorthuysen (1985) observed that *Aurelia* sp. drifted from estuaries in the Wadden Sea out into the North Sea near Den Helder, suggesting that medusae there did not use vertical migration to maintain their position in the estuary. *Aurelia labaita* in Roscoe Bay occupied most of the water column along the entire length of the bay on both large flood and ebb tides (Albert, in press). The scyphozoans *C. hysoscella* and *Rhizostoma pulmo* did not display vertical tidal migration at Den Helder near the entrance to the Wadden Sea (Verwey, 1966).

While vertical tidal migration was not observed with any of four scyphozoans, it did occur in the hydrozoans *Rathkea octopunctata*, *S. tubulosa*, *Eucheilota maculata*, *Aglantha digitale*, and the ctenophore *Pleurobrachia pileus* in the Wadden Sea near Den Helder (Kopacz, 1994).

Table 1
Species typical behaviours of *Aurelia* sp.

Behaviour	Category
Swim up following somatosensory stimulation	Swim away, up
Swim up when encountering low oxygen	Swim away, up
Swim down when encountering low salinity	Swim away, down
Swim down when touching the surface	Swim away, down
Swim down at top 2 m of column water during day	Swim away, down
Swim down and out of turbulence	Swim away, down
Staying away from rocks walls	Swim away
Staying below turbulence	Response inhibition
Horizontal directional swimming	Directional swimming
Remain in areas with the scent of conspecifics	Aggregation
Accumulate in vertical circles	Aggregation
Remain in areas containing the scent of prey	Foraging
Swim faster after capturing prey	Foraging
Swim more variable pattern after capturing prey	Foraging
Swim slower after catching several prey	Foraging

3.11. Summary

Table 1 is a list of *Aurelia* sp. behaviours. I will describe the behaviour categories in the next section.

4. What's is on the mind of a jellyfish?

An *Aurelia* sp. medusa has a lot on its mind. Being mobile in a heterogeneous three-dimensional environment, this medusa has a stream of continuously changing sensory impulses arriving at its central nervous system. These impulses activate neural circuitry that generates sequences of movements. I will now categorize these behaviours as a means of gaining some insight into the neural circuitry of the central nervous system of *Aurelia* sp.

One of the simplest *Aurelia* sp. behaviours was the response to touch by a tentacle of *C. capillata* or by an oyster shell. The medusa responded to the somatosensory stimulus by reorienting itself and swimming up (Table 1; Albert, 2008; Hansson, 1997). Neural circuitry that coordinates feedback from the statocysts with motor output would be needed to execute reorientation and maintain a vertical orientation as the medusa swam upward. I have categorized this behaviour as swimming away and up in response to somatosensory stimulation (Table 1). While the medusa is not swimming directly away from the stimulus, it is swimming in a direction that will avoid further stimulation as opposed to swimming toward a stimulus to increase exposure to the stimulus.

The behaviour of an *Aurelia* sp. following somatosensory stimulation was not rigid. Reorientation depended on the medusa's direction of swimming at the time of somatosensory stimulation. If the medusa was swimming down, it reoriented through 180° but if it was already swimming up, there was no reorientation (Albert, 2008; Hansson, 1997). While somatosensory stimulation was applied for only 1 or 2 s, upward swimming continued for a minute or longer. Accordingly, central neural circuitry must exist that can maintain a stimulus-elicited response in the absence of the external stimulus.

These features indicate that swimming up was not a reflex. A reflex is a relatively unvarying, usually temporally short, pattern of muscle movements like the 1- or 2-s escape response of the hydrozoan *A. digitale* following touch of the bell margin (Mackie, 2004) or the 4-s swimming response by the ctenophore *Mnemiopsis leidyi* following touch by tentacles of *C. quinquecirrha* (Kreps et al., 1997).

Since somatosensory input from different parts of the body were effective in eliciting swimming up, neural circuitry must exist that collects sensory input from diverse areas of the body and brings it to a location where motor control systems are located.

The response to touch depended on the pattern of sensory input. For example, impulses from both mechanoreceptors and chemoreceptors would be sent to the central nervous system when a medusa was touched by a conspecific or a silicone rubber ball (Watson and Hessinger, 1994). Touch by a conspecific or a silicone ball would create different responses in chemoreceptors but a similar response in mechanoreceptors (Oliver et al., 2008; Purcell and Anderson, 1995; Watson and Hessinger, 1994). Touch by a conspecific produced only a pause followed by a resumption of the previous swimming pattern (Hansson, 1997). Touch by the silicone ball initiated reorientation and swimming up (Table 1; Albert, 2008).

Somatosensory stimuli were not the only ones that elicited upward swimming. In Jellyfish Lake (Palau, Hamner et al., 1982) and Elefsis Bay (Greece, Papathanassiou et al., 1987), *Aurelia* sp. have to deal with oxygen levels that diminish with depth. The decrease in numbers of *Aurelia* sp. in the water column with declining oxygen concentration indicates that *Aurelia* sp. swam up in response to low oxygen concentration or a chemical correlate of low oxygen (Table 1; Hamner et al., 1982; Papathanassiou et al., 1987). Where declining oxygen levels were not present, medusae swam down to 40 m in Mljet Lake (Malej et al., 2007) and 30 m in Saanich Inlet (Hamner et al., 1994). The stimuli that terminated downward swimming in these two locations are not known.

Low salinity elicited reorientation and swimming down (Table 1; Albert, 2008; Han and Uye, 2009; Lo and Chen, 2008). There are either receptors that respond to specific levels of salinity or neural circuitry that discriminates between different levels of salinity and initiates a behaviour change at a certain salinity level. The circuitry controlling reorientation must take into consideration the orientation of the medusa at the time the turning down sequence was initiated and coordinate motor activity with feedback from statocysts. Swimming down continued long after a medusa entered water with a salinity greater than 20 ppt. I categorize this behaviour as swimming away and down in response to low salinity (Table 1).

Aurelia sp. frequently avoided the top two meters of the water column during the day, and this behaviour is also categorized as swimming away and down (Table 1; Albert, in press; Han and Uye, 2009; Lo and Chen, 2008; Papathanassiou et al., 1987; Toyokawa et al., 1997). The stimulus that led *Aurelia* sp. to avoid the top 2 m of the water column and that elicited turning down has not been elucidated. In the evening and early morning, upward swimming medusae usually turned and swam down when they touched the surface (Table 1). Frequently, they continued pulsing against the surface, and sometimes they turned down about 10 cm below the surface (Albert, 2008). The variability and complexity of this behaviour identifies it as a species typical behaviour rather than a simple reflex.

Turning and swimming down was also elicited when ebb tides swept *A. labiata* over the gravel bar at the entrance to Roscoe Bay (Table 1; Albert, 2007). The effective stimulus may have been tumbling in turbulent water, vibration, or sound pressure waves. Swimming down has to be modulated by stimuli indicating the depth of the water column. Feedback from the statocysts would be needed to guide downward swimming in the turbulent water. As occurred in response to low salinity, swimming down continued even after medusae entered still water (Albert, 2007). The stimulus that eventually terminated swimming down was not observed.

Staying away from a stimulus is another category of *Aurelia* sp. behaviour (Table 1). When medusae swam down after being swept over the gravel bar at the entrance to Roscoe Bay, they remained below the ebb stream until the ebb flow stopped (Albert, 2008). As the sound pressure waves and vibration would have been subsiding toward the end of the ebb tide, large numbers of medusae accumulated just below the ebb stream. Staying away from the source of a stimulus may require neural control processes that are different from those mediating turning and swimming down. This behaviour appears to be behavioural inhibition—inhibition of moving up into an unoccupied part of the water column.

Staying at a distance from rock walls is categorized as swimming away (Table 1; Albert, 2008). Staying at a distance from rock walls presumably diminished exposure to stimuli associated with being near rock walls. The stimulus mediating the behaviour may be reflected sound pressure waves.

Aurelia sp. remained in an area where there was the scent of prey (Table 1; Arai, 1991). Motor systems presumably make use of sensory feedback from the scent of prey to limit medusae locomotion.

Forming aggregations is a major feature of *Aurelia* sp. behaviour and may be one of the phylogenetically earliest forms of social behaviour. *Aurelia* sp. have chemoreceptors and neural circuitry that allows them to recognize and respond differently to touch by conspecifics compared to touch by a predatory jellyfish (*C. capillata*), a silicone ball, or oyster shells (Albert, 2008; Hansson, 1997; Hansson and Kultima, 1996). It seems reasonable to infer that the sensory receptors and neural circuitry underlying conspecific recognition play a pivotal role in organizing aggregation-forming behaviour.

Directional swimming is a remarkable behaviour that has been observed often (Albert, 2008; Hamner et al., 1994) and in different scyphozoans (Hamner and Hauri, 1981; Shanks and Graham, 1987). This species typical behaviour is guided by feedback from as yet unknown environmental stimuli. The stimulus that terminates the behaviour may be different from the guiding or eliciting stimulus.

Foraging reflects a more complex central nervous system process than the change in swim direction following somatosensory or low-salinity stimulation. Following prey capture, impulses from chemosensors on the oral arms activated central neural circuitry that increased swimming speed, initiated the execution of a prey-search swimming pattern, and then maintained these behaviours for a period of time (Bailey and Batty, 1983). The initiation and maintenance of the behaviour sequence would appear to be controlled entirely by the central nervous system (Table 1). The importance of the continued presence of prey in the lateral tract of the oral arm for maintenance of the behaviour was not examined.

The number and variety of *Aurelia* sp. behaviours (Table 1) suggests that specialized neural circuits may be required to coordinate their execution when more than one behaviour is elicited. For example, a medusa swimming a prey-search pattern will occasionally encounter the surface, low salinity, or a conspecific. Accordingly, the central nervous system of *Aurelia* sp. must have neural circuitry that can intersperse other behaviours within the context of the increased swimming speed and prey-search swimming pattern.

There is at least one situation where the coordination of competing behaviours seems to fail. In Roscoe Bay, *A. labiata* drifted into the estuary at the west end of the bay in the evening when the tide was high (Albert, 2009). At dawn, medusae in other parts of the bay abandoned the top two meters of the water column (Albert, in press), but medusae in the estuary area could not dive down because the water was too shallow. Most medusae in the estuary stayed in the top meter of the water column and drifted out of the shallow area early in the ebb tide (Albert, 2009).

When the depth of the water column reached about 1 m, the few medusae still in the shallow area occasionally dove down, collided with rocks along the bottom, and then swam to the surface (see Section 3.5 above). Diving in the shallow water may reflect a failure of the central nervous system to give priority to responding to the shallowness of the water and inhibiting swimming down. However, the result was adaptive since medusae swam up after colliding with the bottom, entered the ebb flow near the surface, and drifted out of the shallow area (Albert, 2009).

5. Conclusions

Aurelia sp. behaviour is dominated by species typical behaviours. Sensory receptors transmit neural impulses to genetically created neural circuits. These neural circuits generate species typical behaviours rather than simple reflexes.

The behaviours observed were categorized as swimming away from a stimulus and down (low salinity), swimming away from a stimulus and up (somatosensory stimuli), swimming away from a stimulus (rock walls), staying in an area with the scent of food or conspecifics, stimulus guided horizontal swimming, and staying away from a source of sound pressure waves (sound pressure waves associated with turbulence in the ebb stream) (Table 1). Notably missing from the list of observed behaviours is swimming toward a stimulus, such as the scent of food or conspecifics (Table 1).

Foraging appeared to be controlled by more elaborate central neural circuitry. Chemosensory input initiated by prey on the oral arms activated central neural circuitry that increased swimming speed and changed swimming to a prey-search pattern. These behaviours appear to be relatively autonomous, although they were modified by feedback (capture of additional prey).

In order to execute these behaviours, the nervous system of *Aurelia* sp. must contain a variety of specialized receptors and neural circuitry. Among these specialized receptors are those for salinity level, proteins, and the scent of conspecifics. Neural circuitry must exist that coordinates feedback from statocysts with the execution of motor sequences, responds to the pattern of sensory input as well as to stimuli in a single sensory dimension, allows sensory stimuli from many parts of the body surface to elicit a swimming-up response, maintains behaviours after an eliciting stimulus has disappeared, and can inhibit behaviour. The multiplicity of *Aurelia* sp. behaviours suggests the existence of neural circuitry that coordinates the execution of incompatible behaviours.

The behaviours of *Aurelia* sp. are critical to their survival. Their central nervous system is a functionally effective brain that deals with sensory input from several modalities simultaneously, generates behaviours of considerable complexity, and coordinates the execution of incompatible behaviours.

Acknowledgement

The author is indebted to L. Chew, G. Ehman, M.L. Walsh, S. Strand and an anonymous reviewer for constructive suggestions that have greatly improved this manuscript.

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