REVIEW

Olfactory navigation in aquatic gastropods

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ABSTRACT

Gastropod diversity is substantial in marine and freshwater habitats, and many aquatic slugs and snails use olfactory cues to guide their navigation behaviour. Examples include finding prey or avoiding predators based on kairomones, or finding potential mates using pheromones. Here, I review the diversity of navigational behaviours studied across the major aquatic taxa of gastropods. I then synthesize evidence for the different theoretical navigation strategies the animals may use. It is likely that gastropods regularly use either chemotaxis or odour-gated rheotaxis (or both) during olfactory-based navigation. Finally, I collate the patchwork of research conducted on relevant proximate mechanisms that could produce navigation behaviours. Although the tractability of several gastropod species for neurophysiological experimentation has generated some valuable insight into how turning behaviour is triggered by contact chemoreception, there remain many substantial gaps in our understanding for how navigation relative to more distant odour sources is controlled in gastropods. These gaps include little information on the chemoreceptors and mechanoreceptors (for detecting flow) found in the peripheral nervous system and the central (or peripheral) processing circuits that integrate that sensory input. In contrast, past studies do provide information on motor neurons that control the effectors that produce crawling (both forward locomotion and turning). Thus, there is plenty of scope for further research on olfactory-based navigation, exploiting the tractability of gastropods for neuroethology to better understand how the nervous system processes chemosensory input to generate movement towards or away from distant odour sources.

KEY WORDS: Chemosensation, Chemotaxis, Chemoreception, Mollusca, Crawling, Sensory integration

Introduction

Aquatic gastropods are diverse and abundant molluscs, with snails and slugs occupying many different marine and freshwater habitats (Brusca et al., 2016). The Class Gastropoda comprises 40,000 or more species and includes several major subtaxa, all with aquatic members: patellogastropods (true limpets), vetigastropods (abalone and others), caenogastropods (most marine snails), opisthobranchs (sea slugs) and pulmonates (land and secondarily aquatic freshwater snails) (Fig. 1). A variety of lifestyles are found across this diversity. Nutritional modes include omnivores, herbivores and carnivores, some with broad generalist diets and others with extraordinarily specialized diets. Reproductive modes are more stereotyped within subtaxa, with marine species (except opisthobranchs) primarily gonochoristic, while the opisthobranchs and pulmonates are hermaphroditic. Life cycles of most marine species have

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free-swimming larvae, although there are many counter examples of direct development inside an egg case. The latter mode is the norm in freshwater species. Juveniles and adults crawl with a muscular foot, using either waves of muscle contraction or cilia to propel them across substrates (Trueman, 1983). This mode of locomotion (see Glossary) is relatively slow compared with that of many other animal taxa (after accounting for size differences), and thus gastropods are indeed sluggish as they move relative to prey, predators, mates and other important environmental cues.

Navigational behaviour, i.e. patterns of directed locomotion relative to those environmental cues (see Glossary), has been studied in many gastropods. Chemicals are often important for guiding aquatic gastropods, including cues detected by either contact chemoreception or chemoreceptors sampling the water. Indeed, tracking odours (see Glossary) towards or away from their sources is probably one of the most important strategies that have evolved to guide the movement of most aquatic gastropods (Box 1). Thus, neural circuits connecting the olfactory system to either (or both) the muscles and cilia in the foot will form the core control of many navigation behaviours. The primary olfactory organs (see Glossary) thought to be important for navigation are one or two pairs of bilaterally symmetric cephalic tentacles (Fig. 2). Alternatively, some have paired lips or a single fused oral veil overhanging the mouth that is also potentially involved in chemoreception of odours. The osphradium, in or near the mantle cavity in many gastropods, is also chemosensory (Chase, 2002; Lindberg and Sigwart, 2015), but it is not thought to be involved in controlling the direction of movement relative to odour sources. Instead, most studies have suggested it is primarily used to modulate aspects of behaviour and physiology based on the presence (or concentration) of environmental odours (Il-Han et al., 2010; Kamardin et al., 1999; Townsend, 1973b; Wedemeyer and Schild, 1995).

The cephalic sensory organs are probably also mechanosensory, contributing to navigation through detection of both tactile and flow cues. Other sensory modalities may also play roles in navigation, either alone or in combination with olfaction (see Glossary). Eyes are common, with varying complexity and acuity, including some with just a few photoreceptors that presumably only detect general light levels (Chase, 1974; Stensaas et al., 1969) and others at least able to resolve high-contrast features of their environment (Gál et al., 2004; Zieger and Meyer-Rochow, 2008). Non-ocular photoreceptors are also probably widespread (Chono et al., 2002). All gastropods have a statocyst as a vestibular organ, and geosensation is used for movement relative to the water's surface but may also be integrated with olfactory cues to guide movements. Auditory sense organs are not known in gastropods.

Aquatic animals that rely on odours for distant perception are greatly affected by the fluid dynamics of their habitats (Vogel, 1994; Webster and Weissburg, 2009; Weissburg, 2000). Odours can be transported by diffusion or advection, depending on size scales and flow conditions. In conditions with low Reynold's numbers (Fig. 3), odour transport by diffusion is important in generating odour gradients, and flow is slow enough to be laminar (see Glossary),

1

Glossary

Laminar flow
Flow in which there is little mixing among layers of fluid, and thus the layers move in parallel (because the velocity vectors are similar at all nearby points).

Locomotion
Self-generated movement of an animal, resulting in displacement relative to an environmental feature.

Navigation behaviour
Guided locomotion in response to specific cues from abiotic or biotic environmental features.

Navigational strategy
A system of responses to environmental cues that will guide locomotion relative to an environmental feature.

Odour
A mixture of chemicals (odorants) that is different from the surrounding medium.

Olfaction
The action or capacity of detecting odours.

Olfactory organ
An organ involved in the detection of odours (i.e. that performs olfaction).

Turbulent flow
Flow in which there is mixing of nearby fluid layers (because the velocity vector at a given point varies erratically).

producing little mixing. At higher Reynold's numbers, diffusion effects are negligible, and instead faster flow transports odours in turbulent odour plumes. The diversity of aquatic gastropods with regard to both size and the flow conditions they experience spans animals that will have olfactory navigation strategies adapted to diffusive and/or turbulent flow conditions (see Glossary).

This Review summarizes the evidence for how gastropods use odour cues to navigate. The focus is on navigation by slugs and snails crawling over substrates, and excludes navigation behaviour during swimming by either larval stages or pelagic adults. Numerous studies have explored both the proximate and ultimate mechanisms of different behaviours relevant to navigation by benthic gastropods, creating a patchwork of information across species and levels of organization (from subcellular processes to movement patterns of groups of gastropods). A number of past reviews have tackled chemoreception (Croll, 1983; Cummins and Wyeth, 2014; Kohn, 1961) or the neural control of several types of behaviour (Audesirk and Audesirk, 1985; Chase, 2002; Elliott and Susswein, 2002; Willows, 2001). Mucous trail following to find

conspecifics has also been reviewed recently (Ng et al., 2013), indicating it may sometimes involve olfactory navigation. However, to my knowledge, no previous review has attempted to draw together the evidence on navigation patterns with respect to odour cues, the theoretical navigational strategies slugs and snails might be using (Box 1), and the scattered information on relevant sensory systems, central processing and motor systems that could help us to understand how the nervous system produces the behaviours.

Behaviours
Finding food
Olfactory navigation probably contributes to finding food sources in most aquatic gastropods. Many species and diets have been studied, including scavengers, carnivores and herbivores, and both specialists and generalists. As might be expected, olfactory navigation is likely to be critical for scavengers. For example, subtidal whelks (*Buccinum undatum*) were attracted to dead fish from as far as 20 m away in the downstream direction (Lapointe and Sainte-Marie, 1992; McQuinn et al., 1988). In shallow water with minimal flow, marine mud snails (*Ilyanassa obsoleta* syn. *Nassarius obsoletus*), which are normally biofilm grazers, emerge from burial on the mud flat and navigate over tens of centimetres towards crushed shellfish (mussels or another species of gastropod) (Atema and Burd, 1975). Similarly, *Lymnaea stagnalis* and other freshwater snails that are normally herbivorous or graze on biofilms can also opportunistically scavenge, using olfactory cues to localize animal-derived food in the lab (Bovbjerg, 1968; Gray et al., 2009; Madsen, 1992).

Generalist and specialist predators may also rely heavily on olfaction. Marine caenogastropods (*Busycon carica*, *Urosalpinx* spp.) have been shown to be effective olfactory hunters of bivalves or barnacles over distances of 1–2 m (Ferner and Weissburg, 2005; Rittschof and Gruber, 1988). The opisthobranchs *Pleurobranchaea californica* and *Hermissenda crassicornis*, which also have broad diets, use odours to find nearby prey (Avila, 1998; Gillette, 2014; Lee et al., 1974). At the opposite extreme of diet selectivity, the nudibranch *Tritonia diomedea* (which feeds exclusively on pennatulacean soft corals) use olfactory navigation over several metres to find their prey (Wyeth and Willows, 2006a; Wyeth et al., 2006). Other specialist opisthobranchs have similarly been shown to use odours to find food (Cook, 1962).

Some herbivorous gastropods also use odours to find their plant or algal prey. In the lab, the freshwater pulmonate *Biomphalaria glabrata* finds lettuce homogenate and extracts from various aquatic

	Common name	Genera in this Review
Patellogastropoda	Limpets	*Lottia*
Vetigastropoda	Abalone, keyhole limpets top-shell snails	*Haliotis*, *Tegula*
Caenogastropoda	Most marine snails	*Littorina*, *Ilyanassa*, *Buccinum*, *Urosalpinx*, *Amnicola*, *Campeloma*
[Opisthobranchia]	Marine slugs	*Aplysia*, *Tritonia*, *Pleurobranchaea*, *Hermissenda*
Pulmonata	Terrestrial and freshwater snails and slugs	*Lymnaea*, *Biomphalaria*, *Helisoma*, *Radix*, *Planorbella*, *Gyraulus*, *Pomacea*

Fig. 1. Phylogeny of the major gastropod subtaxa, common names and the commonly studied aquatic genera mentioned in this Review.
Opisthobranchia is polyphyletic, including taxa that diverged from multiple ancestors also shared with the Pulmonata. Based on Zapata et al. (2014) and Dinapoli and Klussmann-Kolb (2010).

Box 1. Distinguishing navigational strategies

Several possible navigational strategies have been proposed for gastropods moving towards (or away from) a chemical source. The guidance cues used in the strategies vary, as do the theoretical paths the animals will move should they use these strategies. For more in-depth discussion of the theory behind possible strategies, see Fraenkel and Gunn (1961), Weissburg (2000) and Webster and Weissburg (2009).

Three primary strategies for moving towards a chemical source are considered in this review.

(1) Kinesis: random turns interspersed with straight-line movements. The length (and duration if speed is constant) of the straight-line movements correlate with the detection of increasing chemical concentration, such that despite random headings, the animals will move over time towards the chemical source (strict terminology: chemoklinokinesis). At a minimum, this strategy requires a single chemical sensor for sequential comparison of relative chemical concentrations and also requires stable concentration gradients to be effective.

(2) Chemotaxis: movement in the direction of an increasing chemical gradient. At a minimum, this strategy requires spatially separated sampling of relative chemical concentration (either by moving a single sensor in klinotaxis or comparing two or more sensors in tropotaxis) and also requires stable concentration gradients to be effective.

(3) Odour-gated rheotaxis: movement upstream when a chemical is detected. At a minimum, this strategy requires a single chemical sensor and a single flow direction sensor. It can be effective in any flow environment, with or without stable chemical gradients (as the flow transporting the chemical is what leads the animal to the chemical source).

Integration over time changes the effectiveness of some strategies

If chemical concentration is integrated over time, navigation by kinesis and chemotaxis can become possible in environments where instantaneous stable chemical gradients do not exist. Time integration will reduce random variation in the detection of relative concentrations, allowing reliable detection of concentrations within a noisy gradient. This is particularly important to consider for turbulent environments, where chemical gradients are not stable in the short term, but are present in the average chemical concentration over time. This means that without time integration, animals must rely on odour-gated rheotaxis in turbulent environments, but could use kinesis or chemotaxis if their sensory system can integrate chemical concentrations over time.

Identifying navigational strategies is complicated

Testing which of the three strategies animals may use requires analysis of both cue requirements and movement paths. It is not possible to test which strategy is used simply by manipulating sensory cues or flow conditions, as there is not a 1:1 relationship between cue+flow combinations and navigation strategies. Especially once the possibility of time integration is factored in, multiple strategies may be effective for a given set of cues and flow conditions. For example, in turbulent flow odour plumes, both time-integrated chemotaxis and odour-gated rheotaxis are theoretically effective. In this case, theoretical predictions of navigational paths produced by different strategies (e.g. the random walk of kinesis) are also required to determine which strategy/strategies may be involved. Unfortunately, in some cases, the theoretical differences in navigational paths are subtle (see Fig. 4). Finally, the strategies are not mutually exclusive, and animals may switch between them or employ them simultaneously, further complicating interpretation of experimental results.

plants in both still and flowing water (Bousfield, 1978, 1979; Townsend, 1973a; Uhazy et al., 1978). The marine caenogastropod *Littorina irroratus* showed positive responses to odour from prey plants (Duval et al., 1994). Similarly, *Lymnaea elodes*, another freshwater pulmonate, was attracted towards an aquatic plant in still water in a Y-maze (Gray et al., 2009) (see also Table 1). In aquaria, *Radix ovata* localized sources of several organic compounds isolated from green algae (Fink et al., 2006). Interestingly, *R. ovata* was attracted to chemicals released by damage to the algae, but showed no

attraction to the chemicals isolated from undamaged algae. This somewhat surprising deficit has sometimes been observed in other herbivorous generalists as well, with little or no directed movement towards their intact plant or algal food. *Lymnaea stagnalis* showed no distant response to pieces of an aquatic plant in a Y-maze, and also showed no response when encountering a diffusing gradient of homogenate from the same plant (Bovbjerg, 1968). (Note, however, that there are complexities in interpreting negative results from Y-mazes that diminish the quality of evidence they provide – see Table 1). In the study of *L. elodes* noted above, another freshwater pulmonate *Planorbella trivolvis* (syn. *Helisoma trivolvis*) was not attracted towards an aquatic plant in the Y-maze (Gray et al., 2009). *Aplysia californica*, a marine opisthobranch that feeds primarily on red and green algae (Kupfermann and Carew, 1974; Leonard and Lukowiak, 1986), did not navigate specifically towards food in the lab over anything more than a few centimetres in still water (Teyke et al., 1992). In contrast to earlier reports (Frings and Frings, 1965; Preston and Lee, 1973), Teyke et al. (1992) suggested the animals respond to food odour with increased arousal, moving more quickly but in an effectively random search pattern.

It is important to note that at least some of these studies that failed to find evidence of olfactory navigation towards plant or algal food were conducted in still water. Tests in still water also showed no attraction towards a cocktail of food sources (Dudgeon and Lam, 1985). Truly stationary water rarely occurs in nature, and the animals may be adapted to respond to odour plumes based on flow passing over odour sources. In at least one case, making tests more realistic by adding flow changed the outcome: in a Y-maze with flowing water, *A. californica* were able to localize seaweed prey (Teyke et al., 1992). To my knowledge, no studies have fully addressed how any species of herbivorous aquatic gastropod navigate with respect to prey odour plumes carried by flows verified to be similar to those found in nature.

Avoiding predators

Some slow-moving gastropods respond to predators by retreating into their shells, thereby affecting navigation behaviour by reducing overall movement (Large et al., 2011; Mach and Bourdeau, 2011). However, when shell retreat is less effective, we can expect gastropods to use navigation to avoid encounters with predators. This diminishes the probability of direct mortality and also minimizes the use of potentially costly escape responses (Willows, 2001). Many studies have found that aquatic gastropods indeed seek refuge in various locations, triggered by olfactory cues associated with predators (kairomones) or cues from damaged conspecifics (alarm cues, arising from consumption or digestion of prey by the predator).

A few studies have described directed crawling to avoid predators. In subtidal habitats with continually flowing water, both *Buccinum undatum* and *T. diomedea* respond to odours from their respective sea star predators by heading downstream (Harvey et al., 1987; Rochette et al., 1997, 1997; Wyeth and Willows, 2006a, b; Wyeth et al., 2006). On mud flats, with little or no flow, *I. obsoleta* scatters in all directions away from crushed conspecifics (Atema and Burd, 1975). This last observation highlights one particular aspect of avoidance that has not been thoroughly explored in gastropods. When the goal of navigation is to avoid an odour source, there are multiple possible directions or locations for safety, and thus the behaviour is not simply an inversion of attraction navigation towards a singular source.

The most commonly studied response to predators in gastropods is vertical migration, which moves the snail to aerial habitats that are
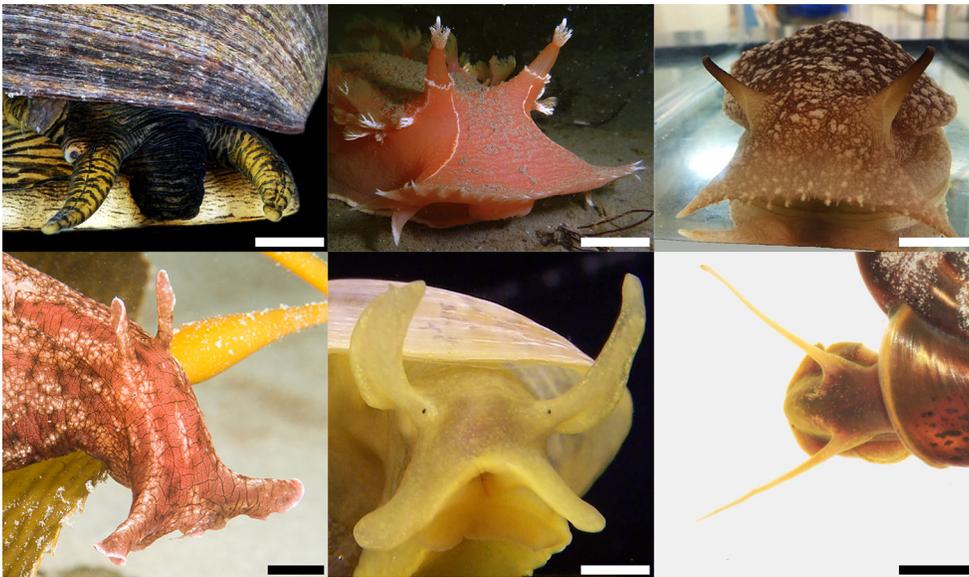
Fig. 2. Examples of gastropod heads and cephalic sensory organs.
(A) *Littorina littorea*. Scale bar: 250 µm.
(B) *Tritonia diomedea*. Scale bar: 1 cm.
(C) *Pleurobranchea californica*. Scale bar: 1 cm. (D) *Aplysia californica*. Scale bar: 1 cm. (E) *Lymnaea stagnalis*. Scale bar: 250 µm. (F) *Biomphalaria glabrata*. Scale bar: 250 µm. See also fig. 1 in Emery (1992). Image credits: A: Ian F. Smith; B: Russell C. Wyeth and James A. Murray; C: Rhanor Gillette; D: Matthew Meier; E: Russell C. Wyeth; F: Tom Kennedy and Coen Adema.

not frequented by their predators. Marine intertidal species, such as *Lottia* spp., *Littorina littorea* and *Tegula funebralis*, move upwards in response to crab or sea star predator odours (Geller, 1982; Jacobsen and Stabell, 1999; Phillips, 1976). Several freshwater species (including *P. trivolvis* and *Lymnaea* spp.) respond similarly to either crayfish or fish odours (Alexander and Covich, 1991a; Covich et al., 1994; Dalesman et al., 2007a,b). Although common, this vertical migration avoidance response is not universal. *Physella virgata* also migrates vertically in response to the combined cue of crayfish along with crushed conspecifics (Alexander and Covich, 1991a,b), but moves under cover in response to fish kairomones (Dewitt et al., 1999; Turner et al., 2000). No upward crawling was observed in response to crayfish-associated odours for the freshwater pulmonates *Helisoma anceps* and *Gyraulus parvus* and caenograstropods *Amnicola limosa* and *Campeloma decisa* (Covich et al., 1994).

Finally, a number of gastropods have responses to predators that are not yet clearly linked to movement patterns, but will probably prove to be part of navigation behaviour. In artificial choice tests, *Littorina scutulata* avoid predator water (Keppel and Scrosati, 2004) and *A. californica* respond to alarm cues in ink released by conspecifics by moving or galloping 'away' (direction was not specified and experiments were conducted in still water) (Kicklighter et al., 2007). Meanwhile, several species (both marine and freshwater) respond to predator odours with burial (Atema and Burd, 1975; McCarthy and Fisher, 2000; Phillips, 1977).

Finding conspecifics

Pheromones for finding conspecifics are probably common in gastropods. In the best-known example, *Aplysia* spp. form breeding aggregations in which animals mate and lay eggs. Both conspecifics and egg cordons are attractive, based on a mixture of pheromones
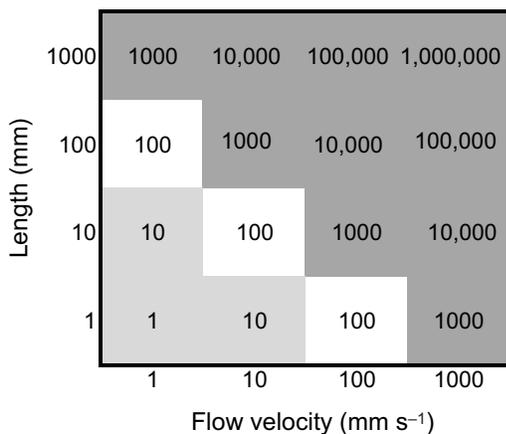
Fig. 3. Matrix of approximate Reynold's numbers for corresponding flow speeds and size scales relevant to aquatic gastropods (Vogel, 1994).
Larger gastropods in faster flows are likely to experience turbulent and inertial flow conditions (dark grey), while smaller animals in slower flows are likely to experience laminar and viscous flow conditions (light grey). Animals with intermediate sizes in intermediate flows may encounter either set of conditions (white).

Table 1. Experiments with flow-through Y- and T-mazes cannot confirm the use of a particular navigational strategy nor refute the ability to detect an odour, owing to multiple possible explanations for positive and negative results

Possible explanations for positive results	Possible explanations for negative results
Odour gradient created between the sides of the choice arena sufficient for chemotaxis towards the side with the odour.	Mixing of flows with and without odours disrupts the odour gradient enough to impede chemotaxis.
Turbulent odour plume only on one side of the choice arena, allowing odour-gated rheotaxis only on the side with the odour.	Mixing of flows with and without odours creates intermittent turbulent odour plumes on both sides, allowing odour-gated rheotaxis on both sides.
	Odorant types or concentrations not detected by the animal, producing no specific response.

Y- and T-mazes allow flow through two upstream arms into a common downstream choice arena. Positive results occur when animals move into the arm with odour significantly more often than they move into the arm without odour (assuming controls show no bias in the absence of any odours in flow).

released from each (Cummins et al., 2006; Susswein and Nagle, 2004). The protein pheromones identified in *Aplysia* have also been implicated in several other gastropods, including *B. glabrata* and the abalone *Haliotis asinina* (Kuanpradit et al., 2010; Pila et al., 2017). In other cases, the pheromones have not yet been characterized. *Ilyanassa obsoleta* have sex-specific responses to at least three different pheromones involved in the formation of mating and egg-laying aggregations (Moomjian et al., 2003). *Littorina littorea* and *Pomacea canaliculata* also have sex-specific responses to sex-specific pheromones (Seuront and Spilmont, 2015; Takeichi et al., 2007). *Biomphalaria glabrata* and *P. trivolvis* also showed intraspecific and interspecific attraction based on odour cues (Marcopoulos and Fried, 1994). All of these studies used T-mazes or other artificial lab environments to test for attractiveness, limiting the information available on the navigational behaviours used in nature (Table 1). Nonetheless, in all cases, the behaviours recorded are similar to food-finding navigation. This is also the case for *T. diomedea* in more natural conditions, which crawled upstream towards conspecifics, presumably in response to a pheromone odour plume, just as they do in prey odour plumes (Wyeth and Willows, 2006a; Wyeth et al., 2006).
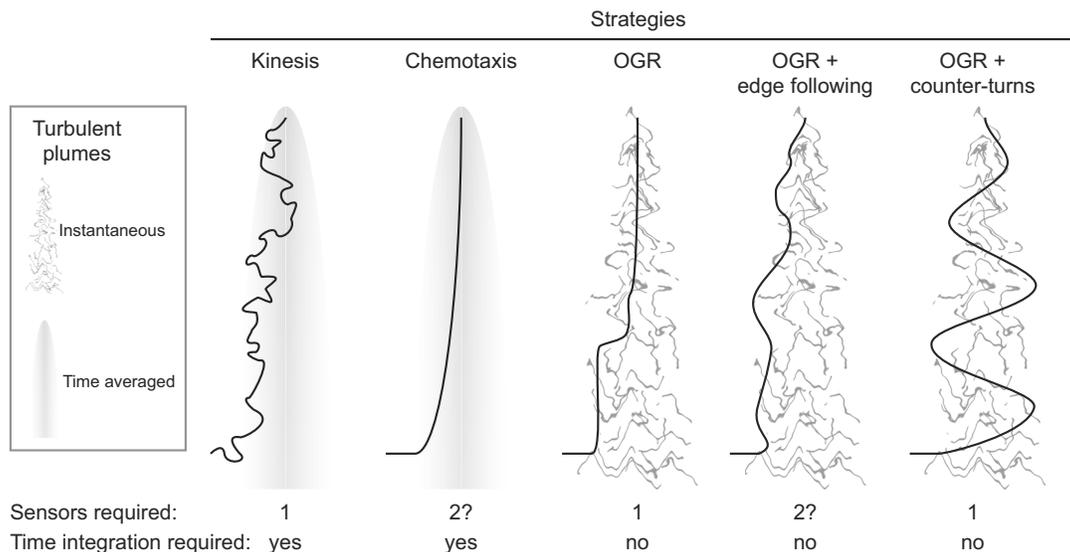
Other

Navigation behaviours may also be involved with moving relative to particular spatial goals that are not prey, predators or mates. Habitat selection, in particular, may invoke navigation behaviours, including homing behaviours to either a preferred habitat or particular home locations. For example, *L. littorea* probably use chemical cues to return to the upper intertidal following dislodgement by wave action (Chapperon and Seuront, 2009). A number of limpet species have preferred locations ('scars' on the rocky substrate surface) to which they return at every high tide. This homing definitely involves

mucous trail following, but several studies have implicated olfaction as well (Cook, 1969, 1971; Ng et al., 2013).

Cues and strategies

Olfactory navigation in aquatic environments can be achieved through three primary mechanisms (Box 1; Fig. 4) (Fraenkel and Gunn, 1961; Webster and Weissburg, 2009). Kineses are typically found in microorganisms, and involve chemical concentration detection but no control of movement heading. Increasing odour concentrations decrease either velocity or the frequency of random turns, allowing organisms moving in random directions to eventually congregate near an odour source. Larger animals, including gastropods, are more likely to use either chemotaxis or odour-gated rheotaxis to head directly towards (or away from) an odour source. Chemotaxis is effective on small scales or in low-flow environments (Fig. 3). Stable concentration gradients (via diffusion and also laminar advection, if slow flow is present) allow spatially separated samples to determine the direction of a concentration gradient, which is then used to guide movement. At larger scales or in higher flow environments, turbulence destroys instantaneous concentration gradients, transporting odour patches downstream in turbulent odour plumes. Thus, most animals seeking an odour source in turbulent flow (see Glossary) use odours to trigger positive rheotaxis, following the flow that transported the odours back to their source. However, slow-moving gastropods present a somewhat complicated case, as temporal integration inside a turbulent odour plume can recover concentration gradients that would permit chemotaxis (Webster and Weissburg, 2001; Weissburg, 2000). Indeed, it is possible that gastropods may use both strategies simultaneously or switch between them depending on flow conditions. The evidence needed to consider these two strategies requires animals be tested in both still and flowing water, and comparison of their navigational paths to instantaneous

Fig. 4. Potential navigation strategies for finding sources of turbulent odour plumes. Some strategies detect the presence of odours only, and thus require just one sensor (see Box 1). Others establish the direction of a chemical gradient, and therefore usually require two sensors (or at least a single sensor that is oscillated in space). Some strategies require only instantaneous sampling of odours, while others rely on time integration to recover the chemical gradients present in a turbulent odour plume over time (Webster and Weissburg, 2001). Kinesis negatively correlates the frequency of random turns to increasing odour concentrations over time. Chemotaxis involves movement in the direction of an increasing odour concentration gradient. Odour-gated rheotaxis (OGR) involves movement upstream in the presence of the odour, and can be augmented by edge-detection mechanisms (following a single edge or counter-turning between the two edges of the plume). The trajectories of gastropods studied to date are most consistent with either chemotaxis based on time-integrated odour detection of chemical gradients or odour-gated rheotaxis without any edge following.

concentration gradients, time-averaged gradients and flow directions (Fig. 4). To my knowledge, this complete set of comparisons has not been accomplished for any gastropod.

Kinesis

There have only been a few laboratory studies where random headings have suggested kineses may underlie odour-based navigation in gastropods. *Littoraria irrorata* showed no bias in turn direction towards prey or predator odours, despite animals showing overall net displacement towards or away from the sources of the odours (Wollerman et al., 2003). This pattern of results has been suggested to be evidence for kinesis (Benhamou and Bovet, 1992). Yet, the tests of *L. irrorata* were completed with odour extracts in seawater pumped slowly into a test arena with otherwise still water – a highly unnatural situation with undocumented flows. Tests of *A. californica* movement in an open field tank, also with no flow, led to speculation of random movement (i.e. a kinesis) rather than a taxis towards their seaweed prey (Teyke et al., 1992). Kinesis was also claimed for several other species of snail (Raw et al., 2013), but the animals did not, in fact, move towards the tested cues, making it unclear how the random movements could be classified as a kinesis. Thus, the evidence for kineses in gastropods to date is limited to a few studies with little or no water movement. It may be that random movement in lab conditions is actually a by-product of strategies adapted to exploit the normally combined effects of odours in flow, and thus the evidence for kinesis is not strong for any gastropod.

Chemotaxis

Unequivocal evidence for chemotaxis is limited in gastropods. A number of studies use the term; however, this is often a semantic mistake as the data indicate only that the animals are using some form of odour-based navigation (e.g. Avila, 1998; Hoover et al., 2012; Lapointe and Sainte-Marie, 1992; Sakata, 1989; Shaw, 1991; Williams et al., 1983). Strictly defined, chemotaxis must involve orienting to chemical gradients. Evidence for chemotaxis requires either testing in completely still water or characterization and comparison of both concentration gradients and movement patterns. Otherwise, it is not easy to distinguish chemotaxis from odour-gated rheotaxis. In absolutely still water, the very slow rate of diffusion (centimetres over hours) casts doubt on the utility of this strategy for all but the smallest gastropods when they are very close to the source (Teyke et al., 1992; Webster and Weissburg, 2009). For example, although observations were made of *I. obsoleta* in shallow water with 'no major water currents noticeable' (Atema and Burd, 1975), the times and distances over which animals responded to the odour of crushed conspecifics indicate that advection must have been involved. Aqueous diffusion of any odour molecule over tens of centimetres requires hours or days, rather than approximately 1 cm min^{-1} as shown in their data. Currents must therefore have advected the odours away from the source. Thus, for the experiments in the same study indicating odour-based navigation towards prey, the animals may have been following concentration gradients generated by a combination of diffusion and advection, or the animals may have been stimulated by prey odour to follow upstream flows (which could have been slow, temporary or meandering, and thus less noticeable). Similar interpretation issues apply to a number of laboratory experiments with little flow (e.g. Bovbjerg, 1975; Fink et al., 2006; Frings and Frings, 1965; Preston and Lee, 1973). Alternatively, numerous studies use Y-mazes or T-mazes (e.g. Avila, 1998; Gray et al., 2009; Willows, 1978), which may provide (unnaturally) steep concentration gradients at the choice point and may be navigable by chemotaxis

or odour-gated rheotaxis (Table 1). In this case, animals may choose the arm of the maze with the odour source either by responding to flow after detecting the presence of odours from that arm or by responding to the concentration difference between the flows emanating from the two arms of the maze. The former is navigation by odour-gated rheotaxis while the latter is navigation by chemotaxis. Thus, positive responses again do not provide clear evidence for which strategy the animals may be using for odour-based navigation.

Odour-gated rheotaxis

Similar complications affect unequivocal identification of odour-gated rheotaxis, even in studies that avoid the problems of little flow or choice mazes (Table 1). Various studies present odours in open-field flow tanks or natural conditions that presumably create turbulent odour plumes (Ferner and Weissburg, 2005; Lapointe and Sainte-Marie, 1992, 1992; McQuinn et al., 1988; Wyeth and Willows, 2006b). But slow-moving gastropods could navigate in such conditions using either odour-gated rheotaxis (based on instantaneous flow and odour cues) or chemotaxis (relying on a temporal average of odour concentration) (Webster and Weissburg, 2001, 2009; Weissburg, 2000). A laboratory study that found evidence of upstream movement in response to various food odours in laminar flow (Bousfield, 1978) is also ambiguous. Finally, studies that used recirculated water in tests for rheotactic responses cannot exclude the possibility of either odour-gated rheotaxis or temporally integrated chemotaxis in response to the animal's own odours (Crisp, 1969; Murray and Willows, 1996).

The distinction between odour-gated rheotaxis and time-averaged chemotaxis has only been included in the interpretation of a few studies. Temporal integration of odour concentrations providing input for chemotaxis has been assumed to be the reason why whelks can handle some more challenging odour plumes (Ferner and Weissburg, 2005; Ferner et al., 2009; Wilson and Weissburg, 2012). However, there is evidence that *T. diomedea* can navigate with a single sensor and without substantial casting (which could permit spatial sampling of any odour gradients), suggesting it probably uses odour-gated rheotaxis (Fig. 4; McCullagh et al., 2014). As both strategies can be effective in odour plumes, categorically distinguishing the two is experimentally challenging (Box 1). Further study of movements relative to both flow direction and time-averaged odour gradients is needed to better understand whether one or both of these strategies are used by different gastropods.

Odour modulation of responses to other cues

Olfactory cues may also be integrated with various other cues to control navigation. The bulk of the evidence involving additional modalities comes from studies that do not directly focus on navigation. Several species of gastropods have been shown to have learned changes in behaviour that involve locomotion (which would then produce effects on navigation). For example, *L. stagnalis* can learn to change its breathing rates, which involves negative geotaxis (leading the animal to the water surface), while *H. crassicornis* can learn to suppress phototaxis. In both cases, the changes in crawling that occur during learning can be influenced by olfactory cues (Alkon et al., 1978; Dalesman et al., 2006; Farley et al., 1997, 2004; Karnik et al., 2012; Lukowiak, 2016; Orr et al., 2007; Rogers et al., 1996). Thus, the odours are not used directly to guide navigation, but rather influence the likelihood (and presumably prioritization) of navigation guided by other cues. Another source of evidence for chemical-induced changes in navigation behaviour comes from numerous ecological studies of how predators influence prey

outside of direct predation. These non-consumptive effects are often mediated by olfactory cues and often involve changed navigation patterns. For example, in the marine snail *T. funebralis*, careful analysis has revealed substantial complexity in potential links between cue types and predation risk that then apparently modulate the degree of locomotion stimulated by predators (Jacobsen and Stabell, 2004). In this and other cases, only the outcomes, such as reduced or increased movement, are known (e.g. Covich et al., 1994; Mowles et al., 2011; Trussell et al., 2002). The results do not capture how exactly navigation with respect to other cues changed after exposure to predator odours, nor the proximate mechanisms by which odours induce those changes. Finally, there is also theoretical support (but as yet no empirical support) for integration of olfactory navigation with magnetoreception for slow-moving animals (such as slugs and snails) relying on odour-gated rheotaxis in variable flow environments (Vasey et al., 2015; Wyeth, 2010).
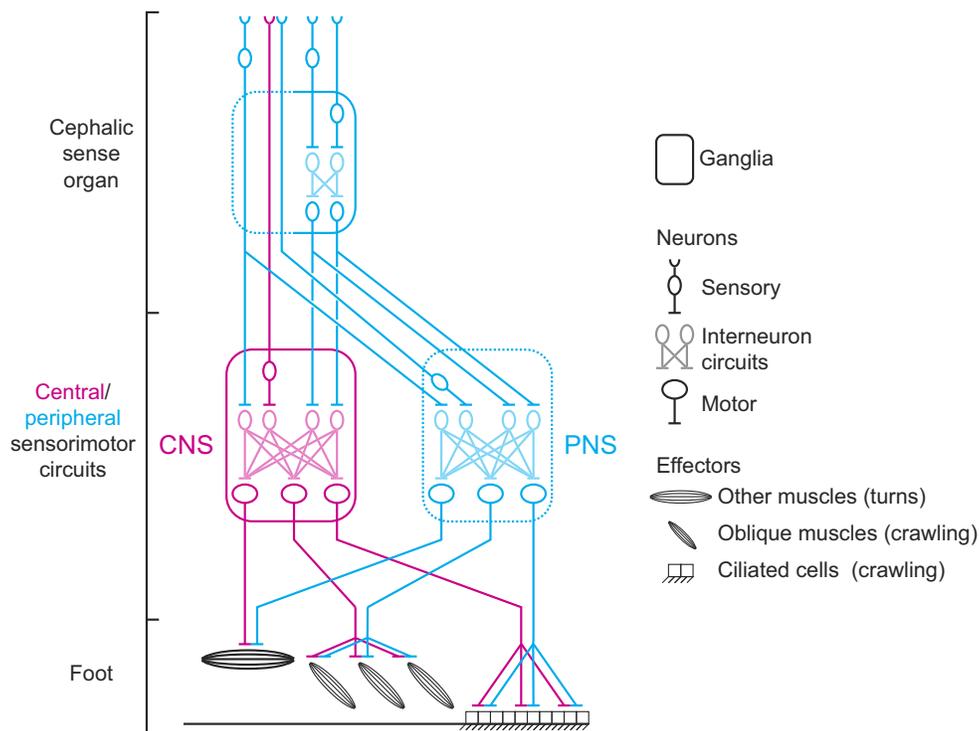
Neural control of navigation

Gastropod nervous systems are both relatively simple and relatively complex, facilitating and complicating the study of circuits that control navigation. Especially within the Euthyneura (the clade comprising the opisthobranchs and pulmonates), central nervous systems have reduced numbers of cells – just tens of thousands of neurons (Chase, 2002). This relative simplicity has aided the extensive study of central neurons and circuits in gastropods. However, the presence of an extensive and diverse peripheral nervous system (Carrigan et al., 2015; Leonard and Edstrom, 2004) creates multiple potential pathways by

which stimuli might trigger behaviour (Fig. 5). Thus, identification of neural circuitry in aquatic gastropods that integrates sensory information about navigational cues to control locomotion needs to consider both central and peripheral neurons.

Sensory neurons

Concrete information is quite limited on many of the sensory cells that provide input to neural circuits that control navigation. Sensory cells in gastropods can be both peripheral (with a dendrite and soma outside the central nervous system and axons projecting centrally) or central (with soma and axon in the central nervous system and dendrites projecting to the periphery). Numerous putative peripheral sensory cells have been identified in a wide variety of gastropods based solely on anatomy (Table 2). However, as these cells have not been amenable to electrophysiological investigation, we know little or nothing about their function. In particular, there are no clear associations between different sensory cell types (as identified by morphology or immunoreactivity) and modality (Wyeth and Croll, 2011). Thus, although we know the cephalic sensory organs of *Aplysia*, *Tritonia*, *Lymnaea*, *Biomphalaria* and other gastropods contain cells necessary for either the control of navigation or at least chemoreception (Audesirk, 1975; Bicker et al., 1982; Levy et al., 1997; Murphy and Hadfield, 1997; Phillips, 1975; Townsend, 1974; Wyeth and Willows, 2006b), we cannot yet specifically identify the cells involved. To my knowledge, no central sensory cells have been linked to the control of navigation behaviours.

Fig. 5. Possible pathways for neural circuits controlling navigation behaviour in gastropods. The cephalic sensory organs contain sensory cells that must be connected to motor neurons controlling muscles or cilia on the foot (either or both can propel crawling, depending on the species) and that must also connect to muscles that generate foot bending during navigational turns. The presence of both a central nervous system (CNS, magenta) and distributed peripheral nervous system (PNS, blue; possibly also including peripheral ganglia) diversifies the potential locations of sensory cell somata, the interneuron circuits they connect to, and the somata of the motor neurons controlling the effectors. The constituents of these theoretical pathways comprise a compilation of central and peripheral anatomy across species, and similarly compiled evidence for the involvement of central and peripheral circuits controlling aspects of different behaviours in diverse gastropods (reviewed in Chase, 2002; Croll, 2003; Cummins and Wyeth, 2014; Leonard and Edstrom, 2004; Leonard et al., 1989; Voronezhskaya and Croll, 2015). A thorough understanding of the neural control of navigation in gastropods includes establishing the necessity and sufficiency of these various possible components.

Table 2. Studies reporting morphological descriptions of peripheral sensory cell types in the cephalic sense organs of different gastropod taxa (not all of which are aquatic)

Neurotransmitter	Taxa	Reports
Catecholamines	*Aplysia*	Croll, 2001; Xin et al., 1995
	Biomphalaria	Vallejo et al., 2014
	Lymnaea	Croll et al., 1999; Voronezhskaya et al., 1999; Wyeth and Croll, 2011
	Phestilla	Croll et al., 2003
Histamine	*Biomphalaria*	Habib et al., 2015
	Helix/Cornu	Hegedüs et al., 2004
	Lymnaea	Wyeth and Croll, 2011
Nitric oxide	*Aplysia*	Moroz and Gillette, 1996
	Lymnaea	Elphick et al., 1995; Serfozo et al., 1998; Wyeth and Croll, 2011
Glutamate	*Lymnaea*	Hatakeyama et al., 2007
FMRFamide	*Limax*	Suzuki et al., 1997
Unknown (structural descriptions only)	*Achatina/Lissachatina*	Chase and Tolloczko, 1993
	Aplysia	Carrigan et al., 2015
	Biomphalaria	Zylstra, 1972
	Helisomal/Planorbella	Yi and Emery, 1991
	Helix/Cornu	Zaitseva, 1994
	Limax	Kataoka, 1976
	Lymnaea	Zaitseva and Bocharova, 1981; Zylstra, 1972
	Phestilla	Croll et al., 2003
	Various	Emery, 1992
	Patellogastropoda and Vetigastropoda	Künz and Haszprunar, 2001
	Opisthobranchia	Göbbeler and Klussmann-Kolb, 2007; Storch and Welsch, 1969

Immunohistochemical methods identify putative neurotransmitters in different cell types, while conventional histology or electron microscopy categorizes types based on structural information.

Motor neurons

Several motor neurons in the central nervous system have been studied using electrophysiological methods in reduced or semi-intact preparations to directly link neural function to specific aspects of locomotion. Two aspects of motor control relevant to navigation have been studied: forward movement and turning. Like many gastropods, *Aplysia* spp. crawl using pedal waves, and various levels of control have been explored, including individual motor neurons controlling rhythmic aspects of foot contraction as well as higher command neurons (Fredman and Jahan-Parwar, 1980, 1983; Jahan-Parwar and Fredman, 1978a,b, 1979a,b, 1980). Other gastropods, such as *T. diomedea* and *H. crassicornis*, use cilia to crawl, and ciliary motor neurons have been identified in both species (Audesirk, 1978; Cain et al., 2006; Crow and Tian, 2003; Popescu and Willows, 1999; Willows et al., 1997). In *L. stagnalis*, crawling can be ciliary or muscular, resulting in two different speeds of locomotion (Korshunova et al., 2016; Pavlova, 2010), although the two systems may have a common serotonergic innervation (but see Longley and Peterman, 2013). Motor neurons controlling turns have also been studied in some gastropods. In *T. diomedea*, identified pedal ganglion neurons have been linked to lateralized muscle contraction that could create lateral bending or lifting of the foot, both leading to a turn during forward locomotion (Murray and Willows, 1996; Murray et al., 1992; Redondo and Murray, 2005). Studies of feeding control in *Aplysia* spp. have also

identified neurons controlling head turns towards food and that may also presumably be involved in turning while crawling (Teyke et al., 1990; Xin and Kupfermann, 1995). In *H. crassicornis*, several pedal ganglion motor neurons controlling foot contractions have been studied (Crow and Tian, 2004, 2009). Although the focus was not on the possibility of lateralized contractions creating bends in the foot for turning, if the motor neurons receive lateralized activation, then they are strong candidates for the motor control of turns during ciliary locomotion. Overall, these various motor neurons are the most promising point of entry for further exploration of the central circuits that control locomotion in gastropods.

Integrative and processing circuits

The most detailed and relevant analyses of integration circuits have focused on responses to combined chemical and tactile stimuli. The natural context of these behaviours has not been thoroughly investigated, but the results presumably apply more to trail-following navigation than to navigation relative to odour gradients or turbulent odour plumes. Gillette and others have established, in detail, how the nervous system in *P. californica* controls turns relative to chemical stimuli applied to the oral veil. The magnitude of both orienting turns toward attractive stimuli and avoidance turns away from aversive stimuli is determined by the position of the stimulus on the oral veil: the more lateral the stimulus, the greater the turn (Yafremava et al., 2007). A single command neuron is necessary and sufficient for production of the behaviour, and the activity of this premotor neuron was itself sustained by a further set of three interneurons (Jing and Gillette, 2003). Collectively, then, this circuit controls the direction and magnitude of the turn. Interestingly, the link between stimulus type (attractive versus aversive) and turn direction (approach versus avoidance) was shown to be labile. Food stimuli usually lead to approach turns, but sometimes trigger avoidance, while noxious stimuli usually lead to avoidance but can trigger approach turns (Gillette et al., 2000). The turn direction for a given stimulus is modulated by satiation level in the whole animal. This appears to operate by a link between the neural circuit controlling feeding and the turn circuit. The evidence indicates that serotonin modulates activity level in the feeding circuit, which then causes a switch in how the turning circuit produces approach and avoidance in response to a given stimulus (Hirayama and Gillette, 2012; Hirayama et al., 2014). Thus, if satiation does indeed change serotonin levels (not proven yet), it could increase activity in the feeding circuit and complete the link between appetitive state and a navigational choice between approaching and avoiding based on chemical stimuli that will be indicative (but not a guarantee) of whether food is nearby.

Little is known about the neural integration used to control navigation in other gastropods. For example, for head turns in *Aplysia* spp., there is a similar link between the laterality of a food stimulus and the magnitude of head turns towards the stimulus (Teyke et al., 1990). Both chemical and tactile stimuli are involved, at least when animals have been aroused by a prior food stimulus. Analyses of the proximate mechanisms behind these responses have been limited to assessing the consequences of lesions to various connectives in the central nervous system and identification of a single central interneuron involved in this and five other behaviours (Xin and Kupfermann, 1995; Xin et al., 1996). Similarly, relatively little is known about how olfaction produces changes in *H. crassicornis* movement towards light. Detailed analyses have explored how interneurons control ciliary crawling, with input from photoreceptors, gravireceptors and tactile receptors (Crow and Tian, 2000, 2002a,b, 2003, 2004). Meanwhile, we know that chemical

stimuli can suppress the likelihood of both spontaneous movement (Ram et al., 1988) and phototaxis (Alkon et al., 1978). However, we have little understanding of the neural circuitry that produces these effects of odours on movement. Moreover, the navigational relevance of the food extracts used as stimuli in these experiments is not clear. Finally, in *T. diomedea*, although the sensory organs that detect the odours and flow used to guide navigation are well characterized (McCullagh et al., 2014; Wyeth and Willows, 2006b), we do not know how this input is integrated to control the crawling and turning motor neurons identified in other studies (Cain et al., 2006; Murray et al., 1992, 2006; Popescu and Willows, 1999; Redondo and Murray, 2005).

Open questions

Predator avoidance navigation behaviour

More detailed analyses are needed of the movements of gastropods relative to predators. These will help us to understand to what degree avoidance navigation is or is not an inversion of attraction navigation. We should also explore the behavioural mechanisms underlying non-consumptive effects of predators on gastropods. Population-level measures of predator avoidance are widespread, but there is little understanding of the changes in navigation by individuals that must lead to changed distributions. The field of neuroecology is beginning to bridge this gap between ecological phenomena and proximate mechanisms of behaviour (Di Cosmo and Winlow, 2014; Murray and Wyeth, 2015; Riffell and Rowe, 2016). As this area of research develops for gastropods, a key requirement will be the use of time-lapse video or other tracking technologies to better characterize the movement patterns of individual slugs and snails in the presence of predators.

Navigation strategies and sensory structures

Several uncertainties remain regarding navigation strategies. The primary questions here are whether chemotaxis or odour-gated rheotaxis or both are used, and in what conditions. Both strategies can work in laminar flow, and with the addition of time integration for chemotaxis, both can work in turbulent flow. No studies to date have fully grappled with the complexities of distinguishing these strategies (Box 1), and thus we still do not have clarity on which strategies are used under which flow conditions during olfactory-based navigation by aquatic gastropods.

Further uncertainties remain with regard to the roles of sensory structures. Chemotaxis probably relies on bilateral comparison of odour concentrations detected by cephalic sensory organs. Odour-gated rheotaxis, in contrast, is theoretically possible without bilateral comparisons, assuming a single sense organ detects odours and flow direction. Thus, one approach to understanding both the site of sensory input for navigation and possible strategies used for navigation is to test whether the animals can navigate with a single sense organ. If they can, this supports odour-gated rheotaxis with all sensory input from the single organ. If they cannot, then both chemotaxis and odour-gated rheotaxis remain possibilities. To my knowledge, this test has only been carried out on one gastropod (McCullagh et al., 2014), supporting odour-gated rheotaxis as the strategy used by *T. diomedea*. Fully unravelling the complexities of sense organs and navigational strategies in different conditions will require testing in both still and moving water, while also manipulating the sensory input available from different sense organs.

Finally, for those gastropods that use odour-gated rheotaxis, how is flow direction determined? The cue is based on circular information, which has implications for detecting both relative changes and absolute headings. To my knowledge, no theories have been proposed for how neural networks could process and code circular flow headings in any animal. Moreover, what is the role of sensory adaptation at the level of both individual sensory cells and higher level circuits? Unlike many sensory cues in other modalities, the relevance of a constant flow stimulus to navigation does not diminish the longer it remains constant. The flexibility of gastropod bodies provides a further layer of complexity for any neural computation of flow heading relative to an animal's locomotion heading.

Neural circuits

Even less is known about the neural underpinning of most navigation behaviours. Some insight into how turns are produced in *P. californica* and other species provides a good starting point. Further work is now needed to understand how odour-induced turns are integrated with the control of crawling (and stopping). Chemotaxis requires inputs from chemoreceptors to determine crawling direction relative to chemical gradients. In contrast, odour-gated rheotaxis requires chemosensory input to modulate motor output for turns relative to flow. Exploration of the neural architecture of both types of navigation is needed. This is probably best pursued by comparing species found in diffusive versus turbulent habitats as well as in species that experience both types of conditions and thus may switch between the strategies. Similarly, comparisons between processing of attractive and aversive odours are needed to establish the overlap and divergence of the circuits controlling these complementary behaviours. In addition, there is a broad scope for investigation of how neural circuits use input from other senses (touch, gravireception, magnetoreception) to modulate responses to odour. Finally, the peripheral nervous system needs special attention for its possible role in controlling navigational responses. Foremost in this area is establishing the modalities of the diverse types of peripheral sensory cells.

Prospective

There is substantial opportunity for further study of olfactory navigation in gastropods. The field has not been the focus for many researchers and, thus, although there is a strong base of relevant behavioural knowledge from past research reviewed here, that information is patchy. For example, we know a fair amount about navigation behaviours towards attractive odour sources, but less about navigation relative to aversive odour sources. Similarly, our understanding of motor aspects of the nervous system substantially exceeds our understanding of sensory systems and processing. This state of the field is quite different to the more concerted study of the neural control of navigation in both insects and vertebrates. Yet, gastropods, because of their sluggishness, provide an important contrast to these faster moving animals. Understanding gastropod navigation (olfactory or otherwise) stands to provide an important contribution to comparative syntheses of navigation across all animals. Moreover, novel technical developments are creating opportunities to fill in the gaps in the existing patchwork of knowledge. Robust and economical camera systems with time-lapse capabilities can be deployed in the field to better capture both natural navigation behaviours and many of the navigational cues (prey, predators and mates) that guide the animals' movements. Either optical recording methods (Frost et al., 2011) or cell-type-specific genetic manipulations (RNA interference, CRISPR/Cas9 and others; Hirosawa et al., 2017; Jiang et al., 2006; Perry and Henry, 2015) need to be explored as better means to study the function of peripheral sensory cells, about which we know so little. Breaking through this barrier is probably a critical precursor for

substantial advances in our understanding of downstream circuits. With more precise information on sensory inputs, both conventional intracellular electrophysiological approaches (in reduced and semi-intact preparations) and modern alternatives, such as multi-unit and implantable recording electrodes (e.g. Cullins and Chiel, 2010, 2010; Hanein et al., 2002; Lu et al., 2013; Saha et al., 2013; Sperry et al., 2018), can be used to unravel the neural circuits that integrate sensory information to control locomotion. Just like the slugs and snails, the field of research may be relatively slow, but much is afoot.

Competing interests
The author declares no competing or financial interests.

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