

## REVIEW

# Rheotaxis revisited: a multi-behavioral and multisensory perspective on how fish orient to flow

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## ABSTRACT

Here, we review fish rheotaxis (orientation to flow) with the goal of placing it within a larger behavioral and multisensory context. Rheotaxis is a flexible behavior that is used by fish in a variety of circumstances: to search for upstream sources of current-borne odors, to intercept invertebrate drift and, in general, to conserve energy while preventing downstream displacement. Sensory information available for rheotaxis includes water-motion cues to the lateral line and body-motion cues to visual, vestibular or tactile senses when fish are swept downstream. Although rheotaxis can be mediated by a single sense, each sense has its own limitations. For example, lateral line cues are limited by the spatial characteristics of flow, visual cues by water visibility, and vestibular and other body-motion cues by the ability of fish to withstand downstream displacement. The ability of multiple senses to compensate for any single-sense limitation enables rheotaxis to persist over a wide range of sensory and flow conditions. Here, we propose a mechanism of rheotaxis that can be activated in parallel by one or more senses; a major component of this mechanism is directional selectivity of central neurons to broad patterns of water and/or body motions. A review of central mechanisms for vertebrate orienting behaviors and optomotor reflexes reveals several motorsensory integration sites in the CNS that could be involved in rheotaxis. As such, rheotaxis provides an excellent opportunity for understanding the multisensory control of a simple vertebrate behavior and how a simple motor act is integrated with others to form complex behaviors.

**KEY WORDS:** Lateral line, Flow orientation, Multisensory, Station holding, Flow refuging

## Introduction

Nearly half a century ago, Arnold (1974) wrote a major review paper on rheotaxis, a widespread orienting response of fish to water currents, typically in the upstream direction (i.e. positive rheotaxis). At the time of Arnold's review – which covered 70 years of published research – vision and, in particular, optic flow cues (see Glossary) were regarded as the dominant sensory cues for initiating and maintaining positive rheotaxis, whereas hydrodynamic flow cues to the lateral line were largely dismissed by Arnold and others (e.g. Dijkgraaf, 1962). Our views on the individual contributions of these two senses have changed dramatically since then. Moreover, we now have a more nuanced view of rheotaxis as an integral part of multi-component behaviors that use multiple senses in species-specific and

flow-dependent ways. Advanced techniques for measuring and visualizing the spatial and temporal characteristics of flow have also revealed the importance of flow characteristics to rheotaxis (e.g. Kulpa et al., 2015) and associated behaviors (e.g. Liao, 2007). Given that fish inhabit a wide variety of flow environments, including creeping flow in small creeks, torrential rivers, wave-swept coasts and huge ocean gyres, a basic understanding of the hydrodynamic principles that govern flow is imperative (see Box 1 for an overview of critical hydrodynamic concepts and terms). This Review (1) places rheotaxis in the broader context of fish behavior in flow, (2) describes how the sensory basis of rheotaxis is determined, including discussion of various methodological pitfalls, (3) summarizes the evidence in support of multisensory contributions to rheotaxis and (4) provides new frameworks for investigating and understanding the sensorineural control of rheotaxis.

## Behaviors associated with rheotaxis

In principle, rheotaxis is a relatively simple orienting response, but in practice, it is combined with other actions to form multi-component behaviors. There are at least three major categories of behaviors associated with positive rheotaxis: goal-directed, station-holding and flow-refuging behaviors. Rheotaxis may also be associated with other miscellaneous behaviors, such as escape actions in response to suction predators (Olszewski et al., 2012). Each of the major categories is discussed in more detail below.

## Goal-directed behaviors

Goal-directed behaviors associated with rheotaxis typically involve biological targets associated with odor cues – e.g. food (Løkkeborg, 1998; Carton and Montgomery, 2003; Gardiner and Atema, 2007, 2014), mates (Johnson et al., 2012) or navigational goals (e.g. natal spawning sites; reviewed in Baker et al., 2002; Gardiner and Atema, 2007, 2014). Whereas a non-directional diffusion process governs the dispersal of odors in still water, odor dispersal in flowing water is dominated by advection and flow dynamics (Weissburg, 2000). Thus, in flowing water, odors can elicit odor-gated rheotaxis, which is used as part of the overall search strategy to locate upstream odor sources. Given that odor is carried downstream by the current, positive rheotaxis is an important directional component of the search strategy.

In addition to these short-range behaviors, the long-range migrations of many diadromous species (see Glossary) like salmonids involve both negative (downstream migration to the sea as juveniles) and positive (upstream migration to natal spawning sites as adults) rheotaxis (Thorpe, 1988; Pavlov et al., 2008). There is an extensive literature on the environmental stimuli and physiological mechanisms involved in long-range fish migrations (reviewed by Hinch et al., 2005), but to our knowledge, little information about the sensorineural basis of negative rheotaxis in this or any other behavioral context. Thus, this Review will focus entirely on positive rheotaxis.

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## Glossary

### Bluff body

A solid body in flow that alters the temporal and spatial pattern of flow.

### Body-motion cues

Sensory cues to visual, vestibular or tactile senses that arise from the downstream advection of the fish by the current; may represent displacement, velocity or acceleration cues.

### Boundary layer

A velocity-gradient region formed at the interface between a solid and fluid over which flow speed increases from zero at the solid's surface to 99% of the freestream velocity.

### Bow wake

The wake created by the leading edge of a stationary bluff body in flowing water or by a moving body in still water.

### Characteristic length

The length of a solid in flow in the direction of boundary layer development, used in computing  $Re$  – e.g. the length of a bluff body or fish in the direction of flow.

### Closed loop

Control operations that use motor outputs (behavior) as sensory inputs (feedback) to the control system.

### Diadromous

Fish that spend part of their life cycle in fresh water and part in salt water.

### Laminar flow

Flow in which fluid particles follow a regular path, moving in more or less the same direction.

### Motor error map

A theoretical construct by which errors between a current and desired motor state are mapped in motor coordinates in the CNS for the purpose of directing corrective actions.

### Open loop

Control operations that do not use motor outputs as sensory feedback to the control system.

### Optic flow

The apparent motion of the whole visual field when there is relative movement between the head and/or body and the surrounding environment.

### Optomotor response

A motor reflex to optic flow.

### Range fractionation

The partitioning of some physical dimension of a stimulus (e.g. flow speed) into different ranges that are covered by different senses or submodalities of a given sense.

### Reynolds number ( $Re$ )

A dimensionless, scaling parameter for predicting different flow regimes; computed from a diverse set of parameters, including flow speed, characteristic length, and fluid density and viscosity.

### Rheophilic

Fish that prefer fast-flowing streams and rivers.

### Turbulent flow

Flow in which fluid particles follow an irregular path, moving in different directions.

### Velocity gradient

Systematic increases or decreases in flow velocity with distance.

### Vestibulomotor response

A motor reflex to head or body motion as sensed by the vestibular system.

### Wide-field

Spatial integration of sensory information over a wide area; panoramic field of view.

## Station-holding behaviors

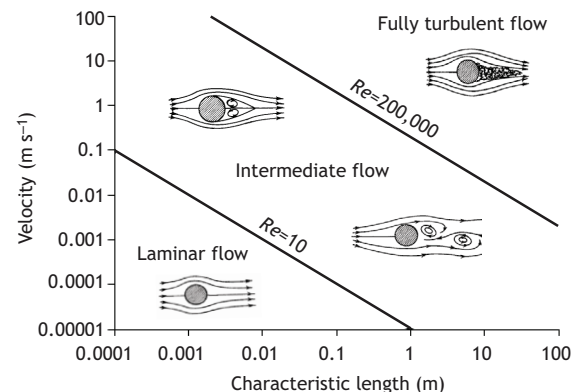
Station holding is defined as the ability of fish to maintain position in a current with respect to a fixed, external frame of reference (Webb, 1989; Gerstner and Webb, 1998). As originally conceived, this term applied to benthic fish holding station on the ground (Fig. 1A–D) (Webb, 1989). However, current speeds sufficiently high to displace fish may cause them to respond by swimming upstream (Webb, 1989)

## Box 1. Important hydrodynamic concepts and terms

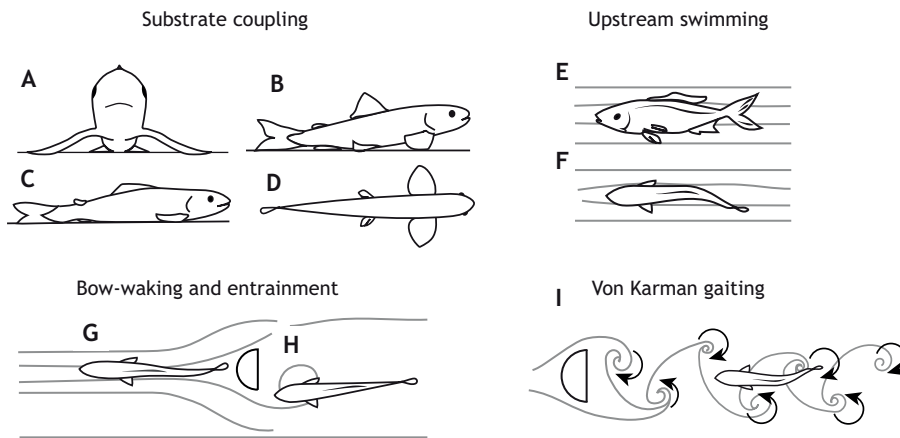
Flow can be described in terms of its temporal and spatial characteristics. Steady versus unsteady flows are distinguished by the absence (steady) or presence (unsteady) of temporal variations in speed, and uniform flow is distinguished from non-uniform flow by the absence (uniform) or presence (non-uniform) of spatial variations in flow velocity (speed and direction). Flow tank boundaries in lab studies, as well as boundaries in natural bodies of water are major sources of non-uniform flow, resulting from boundary-layer effects at the fluid–solid interface. Water jets, created whenever narrow channels of fast-flowing waters empty into larger and slower (or still) bodies of water, are another source of non-uniform flow. In addition, the spatial characteristics of natural currents are often altered by bluff bodies (see box figure), which also introduce boundary layer effects.

Ideally, flow characteristics should be modeled or measured with advanced engineering techniques, such as computational fluid dynamics (Blazek, 2015) and digital particle imaging velocimetry (Thielicke and Stamhuis, 2014). In the absence of these techniques, the Reynolds number ( $Re$ , see Glossary) is a useful tool for predicting the general nature of flow in a variety of circumstances, including behind a bluff body (Vogel, 1994).  $Re$  is a mathematical representation of the ratio of inertial to viscous forces. When viscous forces prevail at very low  $Re$  (e.g.  $Re \sim 10$  for a cylinder; Box figure), boundary layers are thick with shallow velocity gradients and flow is laminar (see Glossary); when inertial forces prevail ( $Re > \sim 200,000$ ), boundary layers are thin with steep velocity gradients, and flow is chaotic and fully turbulent (see Glossary; Vogel, 1994). For intermediate values of  $Re$ , boundary layers and flow patterns are likewise intermediate, being more irregular than laminar flow, but less chaotic and more predictable than full turbulence.

When water viscosity and density are held constant,  $Re$  varies primarily with flow speed and/or the characteristic length (see Glossary) of solids in flow (box figure; see Table S1 for how these factors impact lab studies). By examining the interaction of these two factors, it can be seen that laminar flows are restricted to very slow flows and/or very small characteristic lengths, whereas full turbulence requires very fast flows and/or very large characteristic lengths. In this regard, three points are worth noting. One, the shape and orientation of solid bodies in a current, not taken into full account by  $Re$ , can also impact flow characteristics (e.g. Dutta et al., 2004). Two, turbulence is not well defined in the rheotaxis literature, and it likely represents a wide variety of spatially complex flow patterns in the intermediate flow regime, rather than in the fully turbulent zone. Three, the size of turbulent structures (e.g. eddies, vortices) relative to the size of the fish is an important factor for determining the effects of turbulence on fish (Webb et al., 2010; Cotel and Webb, 2015). For further information on hydrodynamic principles, please see Vogel (1994), Liao (2007) and McHenry and Liao (2013).



and adjusting their swim speed to match that of the oncoming flow, thus exhibiting a different kind of station-holding behavior. Indeed, fish use both substrate coupling (Fig. 1A–D) and upstream swimming



**Fig. 1. Station-holding behaviors associated with rheotaxis.** Substrate coupling by a benthic juvenile salmon from frontal (A), lateral (B,C) and dorsal (D) views (from Arnold et al., 1991 with permission). Postures in A,B and D show behaviors typical of current speeds  $<5 \text{ cm s}^{-1}$ , whereas that in C shows typical posture for flows  $>5 \text{ cm s}^{-1}$ . (E–I) Dorsal views of station-holding behaviors in trout: upstream swimming in uniform, freestream flow (E,F) and bow waking (G), entrainment (H) and von Karman gaiting (I) in the vicinity of a bluff body, modified from Liao (2007).

(Fig. 1E,F) as station-holding strategies to resist downstream displacement. Moreover, a variety of different substrate-coupling behaviors (e.g. body-clamping, downward extension of pectoral fins) and upstream-swimming kinematics (e.g. burst and coast, caudal body and fin undulation) are used by different species to hold station over different flow-speed ranges (Table S2).

For midwater rheophilic species (see Glossary) such as salmon (*Salmo* spp.) and trout (*Oncorhynchus* spp.), there are other kinds of station-holding behaviors in low-velocity regions of disturbed flow around a bluff body (see Glossary; intermediate *Re* zone of Box 1 figure) (reviewed by Liao, 2007; Bleckmann et al., 2012) (Fig. 1G–I). In the bow wake (see Glossary) just upstream of the bluff body, where flow velocity is reduced to zero (the ‘stagnation zone’), fish tend to orient directly upstream while swimming to hold position, a behavior known as ‘bow waking’ (Liao et al., 2003b) (Fig. 1G). Just downstream of the bluff body, flow speed is reduced below ambient, flow direction is opposite to that in the free stream and von Karman vortex wakes are shed (Fig. 1I). Fish exhibit two distinct types of behavior in this downstream region: entrainment, in which they angle their heads and bodies slightly to the left or right side of the bluff body (Sutterlin and Waddy, 1975; Webb, 1998; Montgomery et al., 2003; Liao, 2006; Przybilla et al., 2010; Fig. 1H) and Karman gaiting, in which fish swim in and between the shed vortices to take advantage of their upstream-directed flow (Fig. 1I) (Liao et al., 2003a,b).

### Flow-refuging behaviors

Flow refuging describes how fish avoid the freestream regions of a river or stream in favor of a region of lower current velocity, presumably to conserve energy (Webb, 1998). Thus, station-holding behaviors often take advantage of reduced velocity regions, such as in the wake of a bluff body (Liao, 2007), in the boundary layer (see Glossary) near river beds and banks (Johansen et al., 2007), and near other fine-scale structures such as dips and bumps within margins of a stream (Gerstner and Webb, 1998; Webb, 2006).

### Rheotaxis and associated behaviors in a flow-speed context

Station-holding and flow-refuging behaviors vary according to flow speed and can be broadly grouped into three speed categories: slow, intermediate and fast (Table S2), although the range of absolute flow speeds associated with each category varies with species. Because station-holding behaviors frequently involve feeding on invertebrate drift fauna, the benefits of higher food delivery rates at high flow speeds are likely balanced against the energetic cost of holding station (Hayes et al., 2016). In this respect, bow-waking and entrainment behaviors may also provide greater body stability for visual feeding than Karman-gaiting behavior (see fig. 6 in Liao, 2007).

Among station-holding behaviors, which range from changes in posture to changes in swimming gait (Fig. 1; Table S2), rheotaxis stands out as a common behavioral strategy used by different species and under different flow conditions to conserve energy while resisting downstream displacement. It is the most frequently deployed strategy at low flow speeds and the only behavior that is consistently employed across a wide range of speeds (Table S2). At the low and intermediate end of the flow-speed continuum, rheotaxis is typically associated with substrate-coupling behaviors (Fig. 1A–D), and other station-holding/flow-refuging behaviors in reduced-velocity regions (Fig. 1G–I). At higher flow speeds that cause consistent downstream slippage, rheotaxis is instead associated with upstream swimming (Fig. 1E,F).

### Determining the sensory basis of rheotaxis: metrics and methodological pitfalls

The most common approach to studying the sensory basis of rheotaxis involves comparing the strength of the orienting response in control groups of fish (all senses intact) with those of treatment groups with one or more senses blocked. Several metrics have been used to quantify the strength of rheotaxis. These include the number of (1) fish in a group that are oriented upstream over a given period and (2) times that a solitary individual is oriented upstream over a given period. Two other measures involve the frequency distribution of fish headings (orientations) measured over time, typically for a single fish rather than a group of individuals. These are (3) the vector strength,  $r$ , from circular statistics (Batschelet, 1981) and (4) the rheotactic index (RI), from the cumulative frequency distribution (Bak-Coleman et al., 2013). RI provides a measure of the degree to which rheotaxis is positive (RI=1) or negative (RI=-1), whereas vector strength (and associated statistical tests) provide information on the degree to which headings are randomly ( $r=0$ ) or uniformly distributed in a single direction ( $r=1$ ). Metrics 1 and 2 depend on a criterion for defining upstream (e.g.  $\pm 10$  deg of upstream), whereas metrics 3 and 4 do not. Furthermore, metric 1 can be influenced by pseudo-replication errors and by the packing density of multiple fish in a small tank, where the alignment of fish may be biased along the long axis of the tank and thus, in the upstream (or downstream) direction. Of course, the natural proclivity of some species to form social groups (e.g. schools) needs to be taken into consideration when selecting metrics (Chicoli et al., 2014), as do other natural behaviors of solitary species that tend to compete with rheotaxis (e.g. wall-following behaviors of blind cavefish; Kulpa et al., 2015). Although any of these metrics can be successfully used to determine within-study effects, the use of disparate metrics makes it difficult to draw direct comparisons across studies. Moving forward, criterion-free

metrics (e.g.  $r$  and RI) are preferable when appropriate, because they involve direct measures of orientation and make use of the entire set of sampled data. For further discussion on metrics, see Bak-Coleman et al. (2013).

Methods for disabling various senses in rheotaxis studies are varied (see examples in Tables 1, 2), but many suffer from potential pitfalls. One is the unintended effect of the disabling treatment on the overall behavior of the fish. For example, methods for disabling vestibular senses (e.g. spinning the fish in a centrifuge; Pavlov and Tjuryukov, 1993) make it difficult to distinguish between effects due to the loss of vestibular cues and those due to the inability of the fish to maintain an upright posture. Likewise, pharmacological methods for disabling the lateral line system (Table 1) are subject to the criticism that large doses for extended periods may be toxic and affect the overall health and behavior of the fish (Janssen, 2000). In cases like these, it is important to have independent means of measuring the well-being of the fish or otherwise determining that the observed effect is not due to a general disruption of behavior.

A second major pitfall is that treatments may be partially or entirely ineffective in blocking the desired sense. For example, it is very difficult to block the entire lateral line system by cutting its nerve supply, because this system is spatially distributed all over the

head and body and innervated by up to six different cranial nerves in fishes (Northcutt, 1989). As a second example, the effectiveness of aminoglycoside antibiotics (e.g. streptomycin, neomycin, gentamicin) in blocking the transduction channels of lateral line hair cells is extremely dose-dependent and species-specific, making it imperative to use some means of verifying the effectiveness of the treatment (van Trump et al., 2010; Brown et al., 2011; Kulpa et al., 2015). The fluorescent vital dye (DASPEI), which is actively taken up by the transduction channels of healthy hair cells (Meyers et al., 2003), has become a useful marker for this purpose, as it indicates whether or not the transduction channels are operational (Coffin et al., 2013; van Trump et al., 2010).

A third pitfall of sensory-deprivation approaches is that the absence of an effect does not rule out the possibility that other senses may have compensated for the loss of the disabled sense. This is particularly problematic for body-motion cues (see Glossary and below), which can be encoded by up to three different senses.

### Multisensory cues

Arnold (1974) identified two major categories of sensory cues available for rheotaxis: those that emanate directly from the flow of water around the fish (water-motion cues to the lateral line and possibly

**Table 1. Factors thought to distinguish between studies that provide evidence for and against lateral line-mediated rheotaxis**

Study	Species	Deprivation method	Fish factor 1 (benthic/non-benthic)	Fish factor 2 (sedentary/mobile)	Flow factor 1 (flow-speed dependent/independent)	Flow factor 2 (uniform/non-uniform)
<b>Evidence for lateral line-mediated rheotaxis</b>						
Montgomery et al. (1997)	<i>Cheimarrichthys fosteri</i> (catfish)	Cobalt chloride	Benthic	Sedentary	Dependent (effects below 6 cm s <sup>-1</sup> )	Non-uniform
Baker and Montgomery (1999a)	<i>Astyanax mexicanus</i> (blind cavefish)	Cobalt chloride, physical ablation, gentamycin	Non-benthic	Mobile	Dependent (effects below 10 cm s <sup>-1</sup> )	Non-uniform
Baker and Montgomery (1999b)	<i>Pagothenia borchgrevinnki</i> (Antarctic fish)	Streptomycin, physical ablation	Benthic behavior in experiments	Mobile	Dependent (effects below 6 cm s <sup>-1</sup> )	Non-uniform
Peach (2001)	<i>Heterodontus portusjacksoni</i> (Port Jackson shark)	Physical ablation	Benthic	Sedentary	Flow speed (~3 cm s <sup>-1</sup> ) not varied	Uniform freestream but non-uniform at fish
Berg and Watson (2002)	<i>Astyanax mexicanus</i> (blind cavefish)	EDTA (calcium-free water)	Non-benthic	Mobile	Flow speed not varied	Non-uniform
Suli et al. (2012)	<i>Danio rerio</i> (larval zebrafish)	Neomycin	Non-benthic	Mobile	Flow speed varied over a very low range (0.75–0.2 cm s <sup>-1</sup> )	Non-uniform
Buck et al. (2012)	<i>Danio rerio</i> (larval zebrafish)	Neomycin, streptomycin, gentamicin, cisplatin and salicylates	Non-benthic	Mobile	Flow speed not specified but likely very low	Non-uniform
Bak-Coleman and Coombs (2014)	<i>Corydoras trilineatus</i> (three-lined catfish)	Streptomycin	Benthic	Sedentary	Dependent (effects below 3 cm s <sup>-1</sup> )	Uniform freestream but non-uniform at fish
Kulpa et al. (2015)	<i>Astyanax mexicanus</i> (blind cavefish)	Streptomycin, neomycin	Non-benthic	Mobile	Flow speed in velocity gradient varied ~1–8 cm s <sup>-1</sup>	Non-uniform
Oteiza et al. (2017)	<i>Danio rerio</i> (larval zebrafish)	Copper sulfate, laser ablation of neuromasts and/or lateral line nerves	Non-benthic	Mobile	Flow speed (<1 cm s <sup>-1</sup> ) not varied	Non-uniform
<b>Evidence against lateral line-mediated rheotaxis</b>						
Van Trump and McHenry (2013)	<i>Astyanax mexicanus</i> (blind cavefish)	Gentamycin	Non-benthic	Mobile	Independent (no effect at 1–16 cm s <sup>-1</sup> )	Uniform
Bak-Coleman et al. (2013)	<i>Devatio aequipinnatus</i> (giant danio)	Streptomycin	Non-benthic	Mobile	Independent (no effect at 3 or 7 cm s <sup>-1</sup> )	Uniform
Bak-Coleman and Coombs (2014)	<i>Astyanax mexicanus</i> (blind cavefish)	Streptomycin	Non-benthic	Mobile	Independent (no effect at 1–10 cm s <sup>-1</sup> )	Uniform
Elder and Coombs (2015)	<i>Astyanax mexicanus</i> (sighted Mexican tetra)	Streptomycin	Non-benthic	Mobile	Independent (no effect at 1–12 cm s <sup>-1</sup> )	Uniform

**Table 2. Studies providing evidence that rheotaxis is possible even when one or more senses are blocked or impaired**

Study	Species	Flow condition	Sensory manipulation	Senses blocked or impaired		
				One sense	Two senses	Three senses
Arnold (1969)	<i>Pleuronectes platessa</i> (plaice)	Uniform flow (<5 cm s <sup>-1</sup> )	Tested under light and dark (IR) conditions, were able to orient in the dark when touching tank walls or floor	V		
Hanson and Jacobson (1996)	<i>Oncorhynchus tshawytscha</i> (juvenile chinook salmon) <i>Lepomis macrochirus</i> (bluegill)	Uniform flow (<2.5 cm s <sup>-1</sup> )	Tested under light and dark conditions, were able to orient in the dark when touching tank walls or floor	V		
Pavlov and Tjryukov (1993)	<i>Leuciscus leuciscus</i> (juvenile dace)	Turbulent flow (48 cm s <sup>-1</sup> )	Tested under light and dark conditions with: (1) all senses intact, (2) LL+T blocked with topical applications of MS222, (3) Ve disrupted by centrifuge spin and (4) LL+T+Ve disengaged with methods 2 and 3	V, Ve	LL+T	
Champalbert and Marchand (1994)	<i>Solea solea</i> (larval and juvenile sole)	Non-uniform flow (0.7–20 cm s <sup>-1</sup> )	Tested under light and dark conditions	V		
Kanter and Coombs (2003)	<i>Cottus bairdi</i> (mottled sculpin)	Uniform flow (2–8 cm s <sup>-1</sup> )	Fish blinded by enucleation or lens removal, followed by aspiration of retina; body-motion cues (V, T and Ve) prevented by testing at flow speeds below the slip speed of this benthic, sedentary species			V+T+Ve
Suli et al. (2012)	<i>Danio rerio</i> (larval zebrafish)	Non-uniform flow (<0.2 cm s <sup>-1</sup> )	Tested under light and dark (IR) conditions with LL intact and blocked via immersion of fish in neomycin and EDTA solutions	LL, V		
Bak-Coleman et al. (2013)	<i>Devario aequipinnatus</i> (giant danio)	Uniform flow (3 and 7 cm s <sup>-1</sup> )	Tested under light and dark (IR) conditions with LL intact and blocked via immersion of fish in streptomycin solution	LL, V	LL+V	
Van Trump and McHenry (2013)	<i>Astyanax mexicanus</i> (blind cavefish)	Uniform and turbulent flow (1–16 cm s <sup>-1</sup> )	Tested with LL intact and blocked via immersion of fish in gentamycin solution	V	LL+V	
Bak-Coleman and Coombs (2014)	<i>Astyanax mexicanus</i> (blind cavefish)	Uniform flow (1–10 cm s <sup>-1</sup> )	Tested under light and dark (IR) conditions with LL intact and blocked via immersion of fish in streptomycin solution	LL, V	LL+V	
Elder and Coombs (2015)	<i>Astyanax mexicanus</i> (sighted Mexican tetra)	Uniform and turbulent flow (1–8 cm s <sup>-1</sup> ) (100<Re<1000)	Tested under light and dark (IR) conditions with LL intact and blocked via immersion of fish in streptomycin solution	LL, V	LL+V	
Oteiza et al. (2017)	<i>Danio rerio</i> (larval zebrafish)	Non-uniform flow (<~1 cm s <sup>-1</sup> )	Tested under light and dark (IR) conditions with LL intact and blocked with CuSO <sub>4</sub>	LL, V		

IR, infra-red; LL, lateral line; T, touch; V, visual; Ve, vestibular.

tactile or other cutaneous senses) and those that arise indirectly from the displacement of the fish by the current (body-motion cues to visual, tactile and vestibular senses). Whereas water-motion cues involve flow relative to the fish's body surface, body-motion cues to visual and tactile senses involve the perceived motion of the fish relative to a fixed, external (earth-centered) reference. In contrast, body-motion cues to the vestibular system consist of linear or angular accelerations of the body without requiring land-based fixtures for stimulus generation. In addition to these cues, rheotaxis may be influenced by hydrodynamic or visual cues created by neighboring fish in a school (Chicoli et al., 2014), as well as by visual cues created by the movement of suspended matter or the deflection of aquatic plants in flow. The experimental evidence for different sensory contributions to rheotaxis is summarized below. For background information on each sense, the reader is referred to Coombs et al. (2013) (lateral line), Douglas and Hawryshyn (1990) (vision), Kasumyan (2004) (vestibular) and Kasumyan (2011) (tactile).

#### Lateral line

Despite earlier pieces of evidence in support of a role of the lateral line in rheotaxis (e.g. Dijkgraaf, 1934), the long-standing dismissal of the lateral line as an important player (Lyon, 1904; Arnold, 1974) was not seriously challenged until the seminal studies of Montgomery et al. (1997) and Baker and Montgomery (1999a,b). These studies, conducted on three species of fish (Table 1), showed that rheotactic

performance at flow speeds <6–10 cm s<sup>-1</sup> was reduced to control levels when fish were deprived of lateral line inputs, even when other senses remained functional. The main conclusion of these studies – that the lateral line can mediate rheotaxis – has since received support from independent labs using multiple species and a wide variety of sensory deprivation techniques (Table 1, top rows). Nevertheless, the role of the lateral line in rheotaxis has remained somewhat controversial, owing in part to questions raised about the validity of pharmacological deprivation techniques (Janssen, 2000; van Trump et al., 2010), but also because of several studies that showed opposing results – i.e. no effects of lateral line deprivation on rheotaxis across a wide range of flow speeds (Table 1, bottom rows).

Upon closer examination of numerous variables across all studies, at least two potential flow factors stand out as possible explanations for the seemingly contradictory results (Table 1). The first is the spatial characteristics of flow (i.e. whether flow is uniform or non-uniform). The sources of non-uniform flows in lateral line studies are varied, but are of three general types: (1) water jets, (2) tank–floor boundary layers occupied by benthic fish and (3) boundary-layer challenges in small test arenas with slow flows, as is often the case for larval fish (see Box 1; Table S1). Tellingly, non-uniform flows were used in all ten studies that provided evidence in support of the use of the lateral line, whereas uniform flows were employed in studies that found evidence against such a role. Furthermore, recent studies by Oteiza et al. (2017) show that the lateral line-mediated rheotactic

performance of larval zebrafish (*Danio rerio*) is substantially reduced under zero-gradient flow conditions (i.e. uniform flow), but improves with increasing degrees of non-uniformity (i.e. steepness of the velocity gradient; see Glossary). These findings are consistent with the biophysical properties and known responsiveness of the lateral line to spatial non-uniformities in flow (Kalmijn, 1988, 1989; McHenry and Liao, 2013). Thus, the most parsimonious conclusion from the whole body of evidence is that the lateral line can indeed mediate rheotaxis, but only under non-uniform flow conditions. In this regard, it is worth noting that non-uniform flows are quite common in nature (Liao, 2007).

The second flow factor that may help to explain the conflicting results is flow speed. Four out of ten studies showed that lateral-line deprivation effects were flow-speed dependent, occurring at low, but not high flow speeds (Table 1). Flow speed was not varied for the remaining studies, but was nevertheless quite slow ( $\leq 3 \text{ cm s}^{-1}$ ) in three of these. One interpretation of these results is that there may be an upper limit to the flow-speed range over which the lateral line can mediate rheotaxis. A second, but not mutually exclusive, interpretation is that body-motion cues are absent at flow speeds insufficient to displace the fish, thereby revealing a role of the lateral line. If true, then the question of whether the lateral line can mediate (or participate in) rheotaxis at higher speeds, when compensatory body-motion cues are available, will be difficult to answer without controlling or eliminating additional possible cues.

### Vision

A possible role for optic flow (see Glossary) in rheotaxis was first demonstrated by Lyon (1904); in this study, fish showed optomotor responses (OMRs; see Glossary) that were consistent with rheotaxis. Since then, there have been a plethora of studies documenting the OMR of fish to the rotational motion of the visual surround, typically a series of vertically oriented black and white bars moving around the perimeter of a circular tank in the absence of any real water currents (reviewed in Arnold, 1974 and Bak-Coleman et al., 2015). The typical, but not universal response, is that fish swim in the direction of the optic flow (positive OMR), in a manner consistent with positive rheotaxis. The prevailing explanation of the OMR is that fish reflexively move to stabilize the apparent motion of the visual field (Rock and Smith, 1986).

From these studies, it can be concluded that optic flow elicits OMRs and that, in the absence of other sensory cues, rheotaxis can be explained by this mechanism. However, studies like these do not demonstrate that visual cues are the dominant cues mediating rheotaxis, as was the consensus at the time of Arnold's review. A series of recent experiments by Bak-Coleman et al. (2015) challenged this earlier idea of visual dominance by testing the effectiveness of translational optic flow in eliciting the OMR of larval and adult zebrafish in the presence and absence of uniform water currents. At least two findings from these studies indicate that OMRs may not play as dominant a role in rheotaxis as previously thought. Firstly, although both larval and adult zebrafish exhibit positive rheotaxis to hydrodynamic currents, only young (5–8 days post fertilization, dpf) larvae exhibit positive OMRs consistent with positive rheotaxis. In contrast, older larval (16–18 dpf) and adult fish exhibit negative OMRs. Secondly, in the presence of hydrodynamic currents, optic flow directions in conflict with the direction of the water flow fail to disrupt the rheotactic response of adult fish to the ongoing current. Thus, non-visual cues can override the conflicting optic flow cues.

Perhaps the most compelling evidence against the primacy of optic flow and OMRs in rheotaxis is the fact that eleven studies on

nine different species have shown that rheotaxis is possible in the absence of vision (Table 2). These studies include work on naturally blind cavefish (*Astyanax mexicanus*) and the 5 dpf stage of larval zebrafish, when rheotaxis first appears (see below, 'Sensory cues in larval zebrafish'). In light of the fact that visual cues are largely unavailable at night and even during the day in highly turbid environments, it makes good sense, from an evolutionary perspective, that rheotaxis does not rely exclusively or even predominantly on vision.

### Tactile and other cutaneous senses

In theory, tactile sensors on the body surface of fish, as well as mechanoreceptors associated with cutaneous outgrowths (e.g. fins, barbels) could function as either water-flow or body-motion detectors. Furthermore, it is possible that mechanoreceptors on the ventral surface of benthic fish could detect the sheer stress between the downstream forces of the current and the frictional forces that couple benthic fish to the substrate. Unfortunately, there is currently no direct experimental evidence for any of these possibilities in rheotaxis. Nevertheless, two observations provide circumstantial evidence for a role of tactile senses. The first is that some fish appear to be disoriented when visual cues are eliminated, regaining their rheotactic abilities only after making contact with the substrate or some other stationary surface (Lyon, 1904; Dijkgraaf, 1934; Arnold, 1969; Hanson and Jacobson, 1996). The second observation is that when rheotaxis is experimentally determined to be mediated by the lateral line, fish are either in constant contact with the substrate, as is the case with sedentary, benthic species (Montgomery et al., 1997; Bak-Coleman and Coombs, 2014) or, alternatively, make intermittent but frequent contact with the substrate, as has been observed in the continuously swimming, epi-benthic blind cavefish (Montgomery et al., 1997; Baker and Montgomery, 1999b). In these cases, it has been argued that tactile contact with the substrate provides fish with a necessary external frame of reference (Arnold, 1974; Montgomery et al., 1997; Montgomery and Baker, 2020) (see below, 'External frames of reference and interactions between lateral line, visual and tactile senses').

### Vestibular sense

The most recent experimental evidence in support of the use of vestibular (body acceleration) cues in rheotaxis comes from a pair of studies on juvenile dace (*Leuciscus leuciscus*) by Pavlov and Tjurjukov (1993, 1995; Table 2). In the first study, rheotaxis was shown to persist in both uniform and turbulent flow under varying sensory conditions, including the combined absence of visual, lateral line and tactile cues, indicating that vestibular cues alone are capable of mediating rheotaxis (Table 2; Pavlov and Tjurjukov, 1993). Importantly, rheotaxis was substantially impaired when the vestibular system was also blocked, confirming that sensory information in some form is required. In the second study, Pavlov and Tjurjukov (1995) were able to elicit vestibulomotor responses (VMRs; see Glossary) from multiple fish in a closed, water-filled container that was accelerated in different directions. Fish turned and swam in a direction that was opposite to the direction of imposed motion, but in the expected direction for rheotaxis. Furthermore, this response was retained in the combined absence of visual, tactile and lateral line cues, indicating, as in the previous study, that vestibular cues alone were sufficient for the response.

Recent observations of nocturnal bigeye (*Pempherus adspersa*) in their daytime, reef-crevice refuge provide a strong theoretical case for vestibular cues in rheotaxis (Montgomery and Baker, 2020; Movie 1). These fish respond to the back and forth surges of ocean swell by

orienting upstream during each phase of the alternating current. For alternating currents like these, flow velocity is changing continuously over time in a sinusoidal fashion, first increasing, then decreasing to zero before switching directions. Thus, there is nearly always a substantial acceleration (or deceleration) signal. Furthermore, acceleration peaks in amplitude when the current changes direction, the timing of which is a mere 0.5 s before the bigeye reverse their orientation. Interestingly, bigeye are carried downstream during each cycle of the alternating current, thus minimizing the potential for lateral line cues. As an aside, the absence of station-holding behavior suggests that it is unnecessary and/or energetically inefficient under the circumstances of oscillating flow.

#### External frames of reference and interactions between lateral line, visual and tactile senses

Both visual and tactile senses require a fixed external frame of reference, otherwise body-motion cues derived from the relative motion between the fish and its surrounding environment cannot be generated. In contrast, the use of the lateral line requires relative movement between the fish and the surrounding water, not stationary elements in the surrounding environment. Thus, in theory, lateral line-mediated rheotaxis is an egocentric task – fish need only know the direction of water flow relative to themselves and not relative to something else. However, the same cannot be said for the sensory basis of station-holding behavior, which requires fish to know where they are relative to a fixed external frame of reference.

In this regard, it is instructive to note that midwater species deprived of vision lose their ability to hold position in a uniform current via steady upstream swimming (Fig. 1E,F), but not their ability to orient upstream, although the accuracy of the upstream orientation is slightly reduced (Bak-Coleman et al., 2013; Elder and Coombs, 2015). Without vision, fish move from their typical holding position near the downstream end of the experimental tank to the upstream end, making sweeping, cross-stream movements to the left and right, presumably to maintain tactile contact with the upstream barrier of the tank. The most likely interpretation of these results is that vision is important for station-holding. Thus, when rheotaxis is coupled with station-holding behavior, an external frame of reference becomes important and, in the absence of vision, the tactile sense provides that reference.

Multiple studies on station-holding behaviors in the wake of a bluff body (Fig. 1G–I) show that the interplay between vision and the lateral line is quite complex (Sutterlin and Waddy, 1975; Montgomery et al., 2003; Liao, 2006; Przyzbilla et al., 2010; Bleckmann et al., 2012), making it difficult to determine the precise role of either in rheotaxis. A clear differentiation between rheotactic (orienting) and position-holding (swim speed adjustment, general swimming kinematics) components of these complex behaviors is needed before any conclusions can be reached about the role of these senses in rheotaxis.

#### Sensory cues in larval zebrafish

Positive rheotaxis appears to be an innate and unconditioned response that is observed as early as 5 dpf in larval zebrafish (Olszewski et al., 2012; Suli et al., 2012; Buck et al., 2012; Oteiza et al., 2017) and other species (Champalbert and Marchand, 1994; Champalbert et al., 1994; Masuda and Tsukamoto, 1996). Both lateral line (Raible and Kruse, 2000; Ledent, 2002; Parichy et al., 2009; Liao and Haehnel, 2012; Oteiza et al., 2017) and visual (Easter and Nicola, 1996; Ahrens et al., 2012; Bak-Coleman et al., 2015) systems appear to be sufficiently developed and functional by the time rheotaxis appears. Furthermore, one of these two systems can compensate for the other when input

from either sense is blocked (Suli et al., 2012). However, the loss of both systems leads to substantial impairment of rheotaxis (Suli et al., 2012). Thus, a multisensory foundation for rheotaxis appears to be established as early as 5 dpf. Larval fish at this stage also exhibit both vestibulocular reflexes (eye movement to stabilize gaze during head movement) and touch-evoked startle responses (Easter and Nicola, 1996). However, the role of tactile and vestibular senses in rheotaxis at this early stage is unclear; although by one account, neither is important to lateral line-mediated rheotaxis (Oteiza et al., 2017).

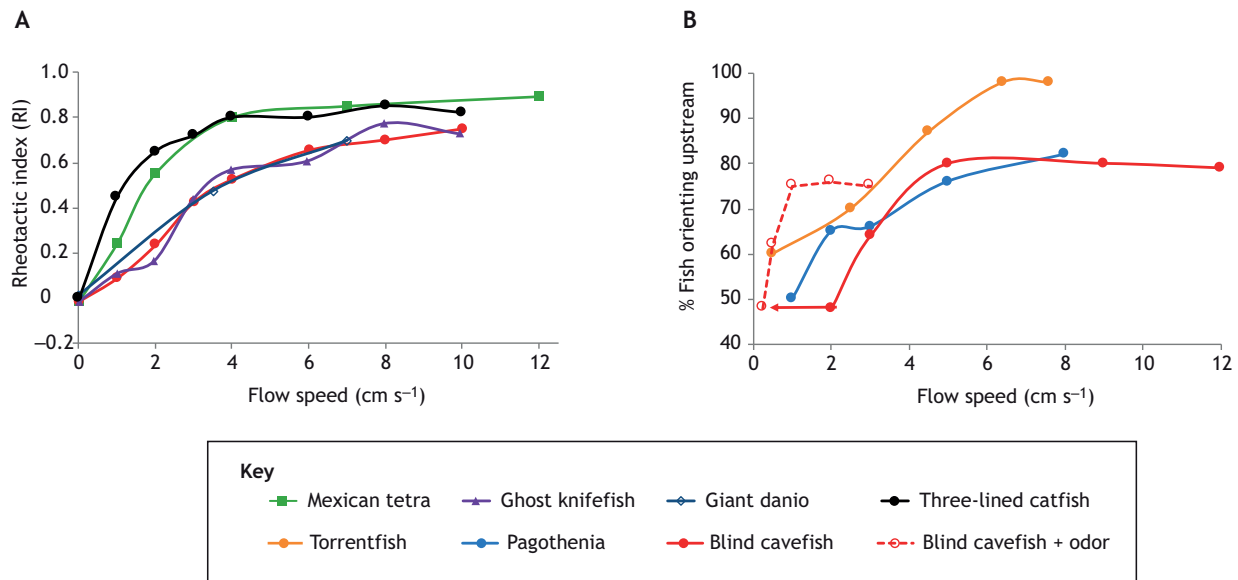
#### A multisensory, range-fractionated framework for rheotaxis

As the previous sections illustrate, there is ample evidence for the use of more than one sense in rheotaxis. Furthermore, multiple studies on different species show that rheotaxis is extremely robust, persisting in the absence of one or more senses, including vision, across a variety of flow conditions (Table 2). Finally, sensory contributions appear to be range-fractionated (see Glossary; Braun et al., 2002), with the contribution of any one sense depending on both sensory and flow conditions. For example, vision may play a substantial role during the day when visibility is good, but not at night when visibility is poor. Likewise, the lateral line may play a substantial role in boundary layer regions, where flow is non-uniform, but not in freestream regions where flow may be more uniform.

In addition, flow speed plays a major role in shaping sensory contributions to rheotaxis. The amplitude of available sensory cues, whether they be water- or body-motion cues, increases with flow speed, as does the strength of the rheotactic response in a wide variety of species under both uniform (Fig. 2A) and non-uniform (Fig. 2B) flow conditions. In addition, body-motion cues become available only when the current speed is sufficiently high to displace the fish. Thus, we suggest that one instructive way to think about the multisensory nature of rheotaxis is along a flow-speed continuum with different modifiable thresholds corresponding to the lowest flow speed at which fish: (1) exhibit an upstream orienting response to the current (orientation threshold), (2) are swept downstream (slip threshold) and (3) begin swimming continuously upstream in an attempt to hold position (upstream swim threshold) (Fig. 3).

The threshold framework that we present here predicts that a different combination of cues will be available during each threshold-bracketed range of the flow-speed continuum. Between the orientation and slip thresholds, fish are not displaced and only the surrounding water moves. Under these circumstances, optic flow and other body-motion cues are unavailable, whereas hydrodynamic flow cues to the lateral line are present and are likely a prominent (if not the sole) source of information about current direction for the purpose of rheotaxis. Somatosensory information may also play a role between the orientation and slip thresholds for benthic fish, even in the absence of body motion, if ventrally located sensors are able to sense the shear stress between the downstream drag forces of the current and the frictional forces coupling the fish to the substrate.

Between the slip and upstream swim thresholds, during which fish are swept downstream by the current, there is theoretically no stimulus to the lateral line if the fish and current move together at the same speed and direction. In this case, body motion cues (see Glossary) – such as optic flow or vestibular cues – must be relied upon. However, body-motion cues can be quite complex in non-uniform flows, as a result of the shear stresses in velocity gradients, which can cause body rotation. Body-motion cues behind a bluff body are particularly complex, with the fish being buffeted about in both linear (heave, surge and slip) and angular (yaw, pitch, roll) directions (Webb, 1998).

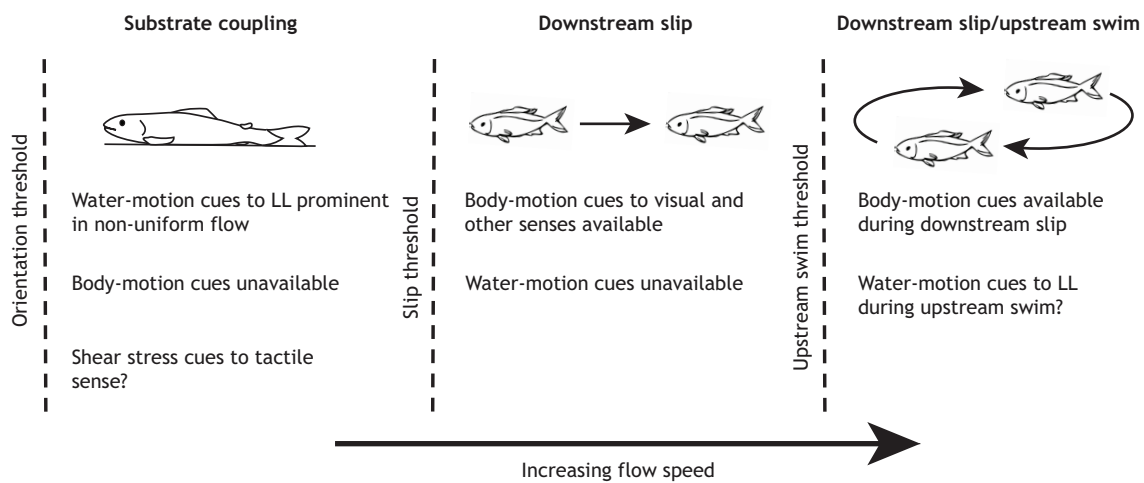


**Fig. 2. Rheotaxis strength increases with flow speed in a wide variety of fish species and flow conditions.** This trend persists in both benthic (black functions) and midwater (colored functions) species, in uniform (A) and non-uniform (B) flow and regardless of whether the metric is the rheotactic index (A) or the mean number (converted to percent) of 4–5 fish orienting upstream (B). In A, data are replotted from Bak-Coleman et al. (2013) (giant danio), Bak-Coleman et al. (2015) (three-lined catfish and blind cavefish), and Elder and Coombs (2015) (Mexican tetra). In B, data are replotted from Montgomery et al. (1997) for all three species and in the presence (dashed red lines) and absence (solid red lines) of odor for blind cavefish (Baker and Montgomery, 1999a,b).

Once the upstream swim threshold is crossed, fish enter a reiterative process in which temporary and intermittent downstream dislocations are followed by compensatory upstream swimming to hold station (Fig. 1E,F; Fig. 3) (see also fig. 8b in Bak-Coleman et al., 2015). Stimulation of the lateral line is theoretically prevented during the downstream but not the upstream phase of the cycle – because net motion between the fish and the surrounding water returns during the latter. Complicating this picture is efferent inhibition of the lateral line system during forward swimming, presumably to nullify self-generated stimulation of the lateral line (Pitchler and Lagnado, 2020). Although beyond the scope of this Review, this raises the important question of how fish distinguish between self-generated and current-imposed water- and body-

motion cues, a topic worthy of its own expansive review (see Montgomery and Bodznick, 2016; Perks et al., 2020).

Orientation, slip and upstream swim thresholds have been measured for several benthic (Table S3A) and midwater (Table S3B) species. Whereas the majority of orientation thresholds occur at a flow of less than 5 cm s<sup>-1</sup>, the majority of slip and upstream-swim thresholds are at flows of greater than 20 and 45 cm s<sup>-1</sup>, respectively. Despite considerable variability in threshold values, a general trend in which orientation thresholds < slip thresholds < upstream-swim thresholds emerges across studies, species and flow conditions. Nevertheless, the trend is clearly better established for benthic than midwater species, owing to the paucity of data on slip and upstream swim thresholds for more neutrally buoyant species (Table S3B).



**Fig. 3. The range-fractionated, multisensory nature of rheotaxis along a flow-speed continuum.** A theoretical framework for understanding the multisensory basis of rheotaxis based on thresholds for measuring the lowest flow speeds at which fish first orient to the flow (orientation threshold), begin slipping downstream (slip threshold) and begin swimming continuously upstream (upstream swim threshold). See text and Table S2 for further details on behaviors associated with rheotaxis in different flow-speed ranges. LL, lateral line.



The operational principles and various traits involved in the modulation of various thresholds are summarized in Box 2. Among these are passive (morphological) traits, such as fish body shape, which can affect both rheotaxis and station-holding abilities. This raises the question of whether passive mechanisms, such as bodies acting like wind vanes when fish are holding station, play a role in rheotaxis. To our knowledge, there is no experimental evidence relating to this question. However, at least two considerations argue against the proposition that rheotaxis is mediated solely by passive mechanisms. The first is that several studies have shown substantial impairment of rheotaxis in both benthic and midwater species when one (Table 1, top rows) or more (Suli et al., 2012; Pavlov and Tjuriyukov, 1993, 1995) senses are blocked. The second is that it is difficult to imagine how freely swimming fish could counteract the multidirectional, destabilizing influences of non-uniform flow without sensory feedback.

### Orienting mechanisms and central control

When thinking about rheotactic mechanisms, several important points should be considered. First and foremost, rheotaxis should not be conflated with station-holding behaviors, in particular upstream swimming (Fig. 1E,F). As a drag-reducing strategy (table in Box 2), rheotaxis is combined with many different forms of station-holding behaviors (Fig. 1; Table S2), but by itself, rheotaxis is an orienting behavior, not a position-holding behavior. Thus, mechanisms for rheotaxis should focus on the sensorineural control of steering movements to maintain body orientation relative to the current rather than on swim-speed adjustments to maintain position relative to a stationary landmark. Furthermore, given that rheotaxis persists in the absence of one or more senses (Table 2) and across a wide range of behaviors, flow speeds and flow conditions (Table S2), mechanisms should be independent of all of these factors. Finally, mechanisms should incorporate what is known about sensory and motor pathways in the CNS and the multisensory integration and processing sites in the brain for orchestrating orienting behaviors (Fig. 4; Coombs and Montgomery, 2014). The orienting behavior may be open loop (see Glossary), as is likely the case for threshold orienting responses of benthic fish at low current

speeds, or closed loop (see Glossary), as is the case when rheotaxis is associated with other types of station-holding behaviors (e.g. upstream swimming) at higher flow speeds (Fig. 1E,F). Based on the above criteria and the available evidence, we propose the following four elements of a multisensory/sensorimotor framework for understanding the sensorineural basis of rheotaxis: (1) motor reflexes to wide-field (see Glossary) water- or body-motion patterns that can be activated by one of several senses; (2) directionally selective, wide-field integration neurons that are tuned to different directions of water or body motions; (3) a multisensory/sensorimotor integration site for constructing a motor error map (see Glossary); and (4) a multifunctional command nucleus in the midbrain that directs central pattern generators in the spinal cord and that integrates instructions for complex and varying behaviors. These are discussed in more detail below.

### Motor reflexes to wide-field flow patterns

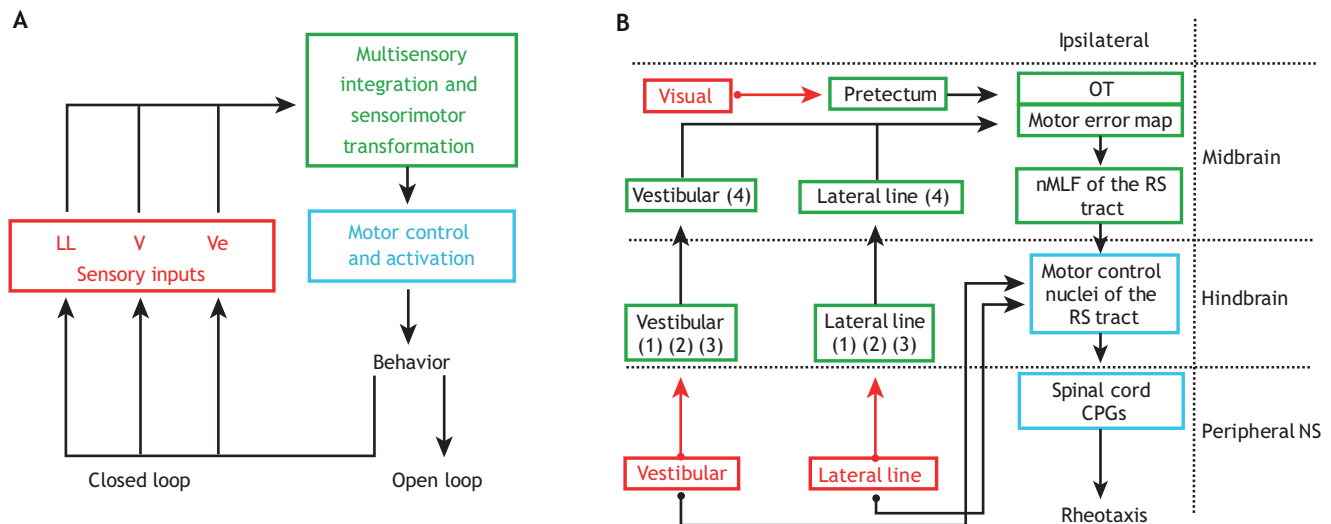
The OMR, as one example of a closed-loop motor reflex to wide-field motion (i.e. optic flow), is instructive for several reasons. One, the OMR has both an orienting (turning) and locomotor (forward swimming with speed adjustments) component that can be differentially activated (Orger et al., 2008; Severi et al., 2014; Thiele et al., 2014). Two, the OMR is an innate, unconditioned response that develops around the same time as rheotaxis in larval zebrafish (Portugues and Engert, 2009; Imada et al., 2010). Three, a more general form of the OMR behavioral algorithm can be applied to all senses for which body-motion cues are available. The general rule is that fish need to adjust their orientation and swim speed in order to nullify the sensory experience of unwanted, imposed motion (Rock and Smith, 1986). In theory, such an algorithm works as a compensatory mechanism for current-induced perturbations of the body in any linear or angular direction and for any body-motion cue, whether it be visual, tactile or vestibular. Indeed, both tactilomotor (Pavlov, 1979, as translated by Kasumyan, 2011) and vestibulomotor (Pavlov and Tjuriyukov, 1995, see above) responses have been observed in fish. In each case, fish turn in response to the perceived tactile or acceleration motion in a direction that is consistent with positive rheotaxis.

### Box 2. Threshold-modulating factors

A number of different factors are involved in the upward or downward shifting of thresholds along the flow-speed continuum (Fig. 3). Food odors have been shown to lower the orientation threshold by a few  $\text{cm s}^{-1}$  in blind cavefish (Fig. 2B) (Baker and Montgomery, 1999b) (Table S3B). In addition, turbulence appears to reduce the orientation threshold relative to that in uniform flow (Elder and Coombs, 2015) or lower levels of turbulence (Pavlov et al., 2000) (Table S3B). Finally, there is some evidence that static magnetic fields can also lower orientation thresholds (Cresci et al., 2017).

Slip thresholds in benthic species can be modified by several operational principles, which implement both passive (biomechanical and morphological) and active (behavioral) traits of the fish (Webb, 1989, 1998; MacDonnell and Blake, 1990; Arnold et al., 1991; Blake, 2006) (see box table). In addition, thresholds can be modified by the boundary layer characteristics of the substrate (Carlson and Lauder, 2010). Comparisons of slip thresholds measured for live and dead fish (Table S3A) indicate that active traits, such as body orientation (rheotaxis), posture (hunkering down) and oral suction can increase the threshold above those determined by passive traits alone (e.g. body density or shape) by as much as  $20\text{--}30 \text{ cm s}^{-1}$  in rheophilic species (Table S3A; Webb et al., 1996; Blake, 2006). Similarly, the characteristics of the substrate can shift the slip threshold upwards. For example, the slip threshold for darters (*Etheostoma* spp.) is substantially higher for rocky ( $55 \text{ cm s}^{-1}$ ) than smooth substrates ( $25 \text{ cm s}^{-1}$ ; Table S3A).

Operational principle	Passive traits	Active (behavioral) traits
Reduces lift forces of the current	Fusiform body shape	Downward angling of pectoral fins to create negative lift
Reduces drag forces of the current	Dorsoventrally flattened body shape	Aligning the body with the current in an upstream direction (rheotaxis); contraction of the tail fin and abduction of paired median fins
Increases frictional coupling to the substrate	Ventral body scales with textured surfaces	Oral sucking
Increases gravitational coupling to the substrate	Decreased body fat, increased body density; reduced size or complete loss of swimbladder	Expulsion of air from the swimbladder



**Fig. 4. Multisensory and motorsensory integration sites proposed for the central control of rheotaxis.** (A) A simplified scheme for closed- and open-loop control of behavior. (B) Corresponding processing sites in the ascending sensory and descending motor pathways of the fish brain. Figure modified from Coombs and Montgomery (2014). Red arrows represent primary afferent inputs from the sensory organs (red boxes), whereas black arrows represent the flow of information (neural projections) to and from various sensory processing regions (green boxes) in the hindbrain and midbrain in relation to motor control regions (blue boxes) in the caudal midbrain, hindbrain and spinal cord. The optic tectum (OT) is divided into superficial layers receiving inputs from the visual system and deeper layers receiving lateral line and vestibular inputs from a 4th order projection nucleus in the midbrain. The deepest layer contains a motor error map for instructing orienting behaviors. See fig. 3.5 in Coombs and Montgomery (2014) for more detailed information on various 1st, 2nd, 3rd and 4th order nuclei in the ascending vestibular/auditory and lateral line sensory pathways. CPGs, central pattern generators; LL, lateral line; nMLF, nucleus medial longitudinal fasciculus; NS, nervous system; OT, optic tectum; RS, reticulospinal; V, visual; Ve, vestibular.

#### Directionally selective, wide-field integration neurons

In the fly visual system, wide-field integration (WFI) neurons are tuned or ‘matched’ to the optic flow fields expected for different rotational and translational directions of body movement (Krapp and Hengstenberg, 1996; Krapp, 2014). Flying insects use this information in various behaviors, for example monitoring ground speed, controlling landings and compensating for the destabilizing effects of air currents (Collett et al., 1993).

In principle, fish could use directionally selective WFI neurons for rheotaxis (Coombs and Montgomery, 2014), and there is evidence that peripheral and/or central neurons across the senses have the requisite response properties – i.e. directional selectivity and integration of sensory inputs over a wide spatial extent. Directionally selective visual neurons in pretectal and tectal areas of larval zebrafish brains encode specific binocular optic flow directions, including both rotational (yaw, roll and pitch) and translational (up and down, forward and backward) directions (Wang et al., 2019). Furthermore, pretectal neurons can apparently distinguish between forward-directed optic flow (that elicits the forward swimming component of the OMR) and sideways flows (that elicit the turning component of the OMR; Wang et al., 2019). Individual organs in the semicircular canals of the vestibular system also show directional selectivity to rotational accelerations of the body, whereas otolithic organs of the inner ear, which have both auditory and vestibular functions, show selectivity to translational accelerations (Goldberg and Fernandez, 1975; Kasumyan, 2004). Prominent hair cell orientation patterns in otolithic organs (Popper and Coombs, 1982; Ladich and Schulz-Mirbach, 2016) predict that directional selectivity falls into three general categories: forward and backward (surge), up and down (heave) and, to a lesser degree, left and right (slip).

Likewise, hair cell orientation patterns in spatially distributed lateral line organs predict directional selectivity to flow motions in forward, backward, up and down directions, with the forward–

backward directions being the most prominent (Schmitz et al., 2008; Chagnaud and Coombs, 2014). Central neurons in a 4th order lateral-line midbrain nucleus (the torus semicircularis, TS), which projects to the optic tectum (OT, Fig. 4), also exhibit directional tuning to the prominent forward–backward directions (Wojtenek et al., 1998). Finally, consistent with wide-field integration, subpopulations of cells in both the first and second order nuclei in the ascending lateral line pathway (Fig. 4) have very broad receptive fields, some of which are even greater than or equal to the length of the fish (Künzel et al., 2011; Engelmann and Bleckmann, 2004; Meyer et al., 2012).

#### A multisensory/sensorimotor integration site

The OT (i.e. the superior colliculus in mammals) is a highly conserved structure in the vertebrate midbrain (Fig. 4B; reviewed in Basso and May, 2017) that controls eye, head and whole-body orienting responses of both adult and larval fish to punctate sources such as prey (Al-Akel et al., 1986; Herrero et al., 1998; Gahtan et al., 2005). Its involvement in orienting responses to whole-field motions, like those proposed for rheotaxis, is less clear: some studies provide evidence for (Springer et al., 1977; Ahrens et al., 2012) and others against (Roeser and Baier, 2003) a role of the OT in the OMR. Nevertheless, the organizational principles of the OT, as described below, can serve as a template for how motor error maps might be constructed for rheotaxis.

The OT receives multisensory inputs, with visual inputs to its most superficial layers and non-visual inputs to deeper layers (Fig. 4). Visual inputs are organized topographically and are in spatial register (physically aligned in the CNS) with similarly organized non-visual inputs. The deepest layers of the OT provide the motor instructions to the descending motor pathway in the form of an egocentric map in motor error coordinates (Fig. 4; Sparks, 1988; Basso and May, 2017). The origin of the coordinate system corresponds to the front of the head, and the motor instructions thus provide information on both the amplitude and direction of

movements needed to bring the front of the head to the object of interest. For positive rheotaxis, the proposed origin of the coordinate system is the upstream orientation, and the motor error map would thus provide information on the turning amplitude and direction (e.g. 40 deg clockwise) required to align the body with the current in an upstream direction.

How are motor error maps for rheotaxis constructed? We propose that different WFI neurons function as matched filters to the desired motor state for rheotaxis, as well as to off-axis states. For the visual system, the desired motor state is motion/orientation in the direction of the optic flow; deviations from the desired state could thus be used to compute a motor error map for closing the gap between the present and desired state. For the lateral line, the desired state for positive rheotaxis is somewhat different – i.e. backward (head-to-tail) water motions. However, if desired and off-axis states for water and body motion directions are in spatial register with each other in terms of the desired state, then inputs from multiple senses could be used individually or in concert to construct a single motor error map. As proof of concept, potential flow theory to model flow signals to the lateral line, in combination with WFI analytical methods, has been used to derive feedback signals (departures from the desired state) that simulate rheotactic behaviors in fish (Ranganathan et al., 2013).

#### A multifunctional command nucleus

The nucleus medial longitudinal fasciculatus (nMLF) has been identified as a distinct midbrain region involved in the control of OMRs in larval zebrafish (Orger et al., 2008; Severi et al., 2014). The nMLF is a cluster of reticulospinal (RS) cells in the caudal midbrain that is part of the descending motor control system in vertebrates (Fig. 4). It is reportedly a multisensory, multifunctional motor command nucleus deployed in a wide variety of behaviors besides the OMR (Sankrithi and O'Malley, 2010), including prey-capture behavior (Gahtan et al., 2005), and general swimming and turning behaviors (Thiele et al., 2014). Both the steering component of the OMR associated with rheotaxis (Orger et al., 2008) and the speed adjustment associated with upstream swimming to hold station (Severi et al., 2014) are controlled by this nucleus and can be independently activated. Furthermore, the turning component of the OMR has been shown to be strongly tuned to optic flow direction (Orger et al., 2008). The nMLF also receives inputs from the OT (Gahtan et al., 2005), and its neurons project to hindbrain motor areas, which in turn project to central pattern generators in the spinal cord (Fig. 4).

#### Summary and conclusions

Rheotaxis is one of many behavioral strategies that fish use to conserve energy while resisting downstream displacement. However, among these strategies, rheotaxis is the most versatile and widely applicable across species and flow conditions. Information about current direction is provided predominantly by water motion cues to the lateral line and body motion cues (when fish are displaced downstream) to visual, vestibular and tactile senses. The use of lateral line versus other sensory cues is determined by multiple factors, including sensory condition (e.g. visibility), the spatial characteristics of flow (uniform or non-uniform) and by three modifiable thresholds defined by the lowest flow speed at which fish: (1) first orient to the flow, (2) become displaced by the flow and (3) begin swimming upstream against the flow.

All the available evidence indicates that rheotaxis depends on more than one sense in a range-fractionated way. When sensory and flow conditions are unfavorable for one sense, other senses compensate. As such, rheotaxis persists under a wide range of

conditions and is remarkably resilient to the loss of information from one or more senses. In this Review, we have proposed a multisensory framework for understanding the sensorineural basis of rheotaxis. This framework involves motor reflexes to water or body motions and CNS neurons that are tuned to different directions of wide-field motion. A single motor error map, constructed from in-register contributions of WFI neurons in multiple senses, provides instructions for closing the gap ('error') between the fish's current orientation state and the desired state (directly upstream). With the advent of whole-brain imaging techniques and other advantages of working with larval zebrafish (e.g. closed-loop manipulations of sensory feedback), it may soon be possible to map out the complete neural circuitry – from stimulus input to motor output (and back again in closed-loop fashion) – of a relatively simple, but multisensory vertebrate behavior. Even more exciting is the possibility of learning how the sensory inputs and motor instructions for rheotaxis are seamlessly integrated with those for station-holding and other more complex behaviors, especially those in non-uniform flows.

Moving forward, many questions remain unanswered. For example, what role, if any, do passive (e.g. wind vane) mechanisms play in rheotaxis and how are these influenced by fish factors (e.g. body shape) and flow dynamics? What more can be learned about the potential role of vestibular, tactile and other cutaneous mechanosenses in rheotaxis? What about negative rheotaxis: is there a polarity switch in the brain somewhere that goes from positive to negative? Or, is positive rheotaxis a fixed reflex that is merely inhibited during negative rheotaxis? Do motor error maps play a role in rheotaxis and, if so, where in the CNS are they constructed and exactly how are they constructed? The answers to these and many other questions will add an exciting new chapter to a century-old area of research.

#### Competing interests

The authors declare no competing or financial interests.

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#### Supplementary information

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