

The role of the lateral line and vision on body kinematics and hydrodynamic preference of rainbow trout in turbulent flow

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Summary

The ability to detect water flow using the hair cells of the lateral line system is a unique feature found in anamniotic aquatic vertebrates. Fishes use their lateral line to locate prey, escape from predators and form cohesive schooling patterns. Despite the prevalence of complex flows in nature, almost nothing is known about the function of the lateral line and its relationship to other sensory modalities for freely swimming fishes in turbulent flows. Past studies indicate that under certain conditions the lateral line is not needed to swim steadily in uniform flow. This paper examines how the lateral line and vision affect body kinematics and hydrodynamic habitat selection of rainbow trout (*Oncorhynchus mykiss*) exposed to vortices generated behind a cylinder. Trout Kármán gaiting (i.e. exploiting vortices to hold station in a vortex street) with a pharmacologically blocked lateral line display altered kinematics; body wavelength and wave speed increase compared to control animals. When visual cues are withheld by performing experiments in the dark, almost all Kármán gait kinematics measured for fish with and without a functional lateral line are the same. The lateral line, rather than vision, plays a larger role in affecting body kinematics when trout hold station in a vortex street. Trout show a preference to Kármán gait in the light but not in the dark, which may be attributed to physiological state rather than hydrodynamic or sensorimotor reasons.

In the dark, trout both with and without a functional lateral line hold station near the downstream suction region of the cylinder wake (i.e. entraining) and avoid the vortex street. Vision therefore plays a larger role in the preference to associate with a turbulent vortex street. Trout in the light with a blocked lateral line show individual variation in their preference to Kármán gait or entrain. In the dark, entraining trout with an intact lateral line will alternate between right and left sides of the cylinder throughout the experiment, showing an ability to explore their environment. By contrast, when the lateral line is blocked these fish display a strong fidelity to one side of the cylinder and are not inclined to explore other regions of the flow tank. Both entraining and Kármán gaiting probably represent energetically favorable strategies for holding station relative to the earth frame of reference in fast flows. The ability to decipher how organisms collect and process sensory input from their environment has great potential in revealing the mechanistic basis of how locomotor behaviors are produced as well as how habitat selection is modulated.

Key words: lateral line, vision, turbulence, kinematics, behavioral choice, Kármán gait, entraining, rainbow trout, vortices, cobalt chloride.

Introduction

Turbulent flow is generally thought to destabilize swimming trajectories and increase the cost of locomotion for fishes (Enders et al., 2003; Pavlov et al., 2000). However, under certain flow conditions fishes have shown an ability to exploit unsteady flows to enhance swimming performance, thereby turning an environmental constraint into a benefit (Breder, 1965; Hinch and Rand, 2000; Streitlien and Triantafyllou, 1996; Webb, 1998; Weihs, 1973). Recent studies have found that trout swimming in an experimentally generated vortex street showed unique kinematics, termed the Kármán gait,

which is accompanied by a decrease in red axial muscle activity (Liao, 2004; Liao et al., 2003a). The Kármán gait illustrates the ability of fish to recycle fluid momentum from oscillating flows to exploit a passive mechanism of thrust generation (Beal et al., 2006; Liao, 2004). Yet while the intrinsic compliance of the musculoskeletal system can facilitate the passive use of vortices, it is clear that to maintain this behavior for an appreciable amount of time requires active control. Any comprehensive study aimed at understanding how the physical environment influences organismal behavior must integrate biomechanics with how organisms sense and process their

dynamic environment. This approach serves as an entry point to better understand the basis of higher order processing such as the ability to choose habitats.

Complex water currents are common in nature, can be detected by the lateral line (Engelmann et al., 2002; Engelmann et al., 2003; Mogdans and Bleckmann, 1998; Montgomery et al., 2003; Vogel and Bleckmann, 2000), and exert a large affect on swimming kinematics and behavior (Fausch, 1993; Gerstner, 1998; Heggenes, 2002; Liao et al., 2003a; McLaughlin and Noakes, 1998; Webb, 1993; Webb, 1998). However, surprisingly little is known about how turbulence levels affect the sensorimotor control of freely swimming fishes.

Fishes are able to detect hydrodynamic pressure differences created by flow velocity gradients with the mechanosensory hair cells of their lateral line system (Coombs et al., 1989; Dijkgraaf, 1963). The ability of the lateral line to encode hydrodynamic information plays a critical role in many fundamental behaviors such as rheotaxis (Dijkgraaf, 1963; Kanter and Coombs, 2002; Montgomery et al., 1997), predator avoidance (Blaxter and Fuiman, 1989), prey detection and capture (Conley and Coombs, 1998; Coombs et al., 2001; Montgomery and Coombs, 1998) and schooling behavior (Pitcher et al., 1976). The broad utility of the lateral line system stems from two different receptor classes, which are sensitive to different flow characteristics (Coombs et al., 1989), providing the ability to detect hydrodynamic stimuli even in the presence of background flow (Engelmann et al., 2000). Though it is tempting to speculate that the ability to sense and control body-generated vortices may enhance the efficiency of undulatory locomotion, the data suggest that the kinematics (S. Coombs, E. Anderson, J. Montgomery and M. Grosenbaugh, personal communication) and performance (Dijkgraaf, 1963) of freely swimming fish in uniform flow remain unaffected when the lateral line is blocked. Electrophysiology experiments on paralyzed, aquatic vertebrates show a default pattern of sequential, rostrocaudal motor activity that proceeds without any sensory feedback (Masino and Fetcho, 2005; Soffe, 1993). Thus, the known function of the lateral line as a flow detector is seemingly at odds with its non-essential role during swimming in uniform flow (this should not to be confused with initiation of swimming). It is possible that perturbed flows provide a more revealing context to determine the role of the lateral line during locomotion. We currently lack any kinematic data of freely swimming fishes in the presence of known hydrodynamic perturbations (but see Montgomery et al., 2003; Sutterlin and Waddy, 1975), which precludes us from understanding what type of hydrodynamic information the lateral line provides in turbulent conditions. By exposing fish to periodic vortices shed behind a cylinder in the light and dark, this study addresses a fundamental question about which sensory cues are important to accommodate unsteady flows and how this affects the selection of hydrodynamic habitats.

Like most vertebrates, fishes are predominantly visual animals and can rely on vision to initiate and modulate locomotion (Douglas et al., 1989; Fernald and Wright, 1985;

Hobson et al., 1981; Roeser and Baier, 2003). Yet behaviors are almost always shaped by multiple sensory modalities and studies have recognized the importance of simultaneous contributions of vision and the lateral line during locomotion (Janssen and Corcoran, 1993; Montgomery et al., 2003; Partridge and Pitcher, 1980; Sutterlin and Waddy, 1975). A goal of this study was to determine how the lateral line and vision affect the ability and preference of fishes to swim in the hydrodynamic flow environments established around a stationary cylinder placed in uniform flow. For example, are Kármán gaiting fish relying on their lateral line to generate corrective motions to maintain position in vortical flows? This study investigates whether trout significantly alter Kármán gait kinematics when either the lateral line or vision is blocked. In addition, it examined how the presence or absence of the lateral line and vision affects the preference of fish to associate with different hydrodynamic environments around a stationary cylinder in flow.

Materials and methods

Animals

Rainbow trout *Oncorhynchus mykiss* (Walbaum) were obtained from a commercial hatchery in western Massachusetts, USA. Fish were held in a 1200 l circular freshwater tank ($15 \pm 1^\circ\text{C}$, mean \pm s.e.m.) with constant flow, on a 12 h:12 h light:dark cycle and fed commercial trout pellets daily. Four trout were used in the experiments, with a total body length (*BL*) of 16.6 ± 0.4 cm (mean \pm s.e.m.). Additional data from four separate animals were incorporated from previous studies to confirm that fish exposed to the experimental setup on consecutive days did not alter their swimming kinematics as a result of prior exposure.

Pharmacological block of the lateral line

Fish were exposed to 0.15 mmol l^{-1} cobalt hexachloride (Sigma-Aldrich Corp., St Louis, MO, USA) in calcium-free de-ionized water (15°C) for 3–4 h to block specifically the mechanosensory hair cells of the superficial and canal neuromasts without affecting the function of the inner ear (Karlsen and Sand, 1987). The minimum concentration of cobalt chloride (J. Engelmann, personal communication) and exposure time (Baker and Montgomery, 1999; Montgomery et al., 1997) needed to block the lateral line were initially obtained from the literature. Since fish were exercised after the cobalt treatment, concentrations and exposure times needed to be adjusted from previous studies in which fish were not exercised. These values were empirically adjusted by systematically exposing trout ($N=12$) to varying cobalt concentrations and exposure times with the following criteria; (1) fish would survive after the experiment and resume normal swimming and feeding activity within 3 days, and (2) fish would display an escape response to a sudden jet of water from a syringe prior to treatment but not after.

Pharmacological blocking of the lateral line has been widely used (Baker and Montgomery, 1999; Coombs et al., 2001;

Janssen and Corcoran, 1993; Montgomery et al., 1997) and is less invasive and more comprehensive than physically severing the lateral line nerve (Dijkgraaf, 1973). Care must be exercised to avoid negatively affecting the health of the fish, since toxic side effects may alter behavior, which is then erroneously attributed to a blocked lateral line (see Janssen, 2000). The applied concentration of a pharmacological agent should be experimentally titrated and monitored so that it reveals an effect, as determined by a behavioral or physiological assay, but is not detrimental to the health of the fish. For example, treated fish in this study often fed during the experiment, providing independent verification that normal behaviors remained intact after treatment.

To confirm that the cobalt chloride treatment blocked the lateral line, before each experiment a hand-operated syringe was slowly positioned behind a treated fish swimming steadily in uniform flow. A 30 ml jet of water was quickly discharged at the caudal half of the body to elicit an escape response (Fig. 1). Since the experimental flow tank did not contain cobalt chloride, after an experiment (typically 1–3 h) the response of the fish to a jet of water was again recorded to ensure that the cobalt treatment had not yet worn off. Kármán gait kinematics and body position relative to the cylinder were recorded for all four experimental treatments.

Twenty-four hours before each experiment, an individual fish was selected and isolated in a partitioned chamber in the holding tank. On the morning of the experiment, the fish was removed and brought to the experimental room to be treated with cobalt or left untreated depending on the stage of the experiment. The transportation and handling of untreated and cobalt-treated fish to and from the experimental flow tank were identical to avoid possible behavioral differences due to handling.

Infrared experiments

Two 20×20 infrared (IR) light emitting diode (LED) arrays (850 nm, BG Micro Co., Garland, TX, USA) were used to illuminate a white Plexiglas background above the flow tank. This wavelength was chosen because the retinal cones of rainbow trout cannot detect wavelengths above 750 nm (Hawryshyn and Harosi, 1994). A Sony DVR TR-38 Nightshot Camcorder (30 frames s⁻¹) aimed at a 45° front-surface mirror placed below the flow tank recorded the ventral view of the trout against the IR-lit background. The camcorder imaged the entire working area of the flow tank (25×80 cm), and custom written software (Image Acquisition Toolbox, Matlab v6.5; Mathworks, Natick, MA, USA) continuously recorded the position of the head every 5 s for 1 h to obtain positional preference data. An IR-sensitive Redlake camera (60 frames s⁻¹, 1/125th second shutter speed; Tucson, AZ, USA) imaged the region of the vortex street behind the cylinder to capture detailed Kármán gait kinematics. For experiments performed in the dark, the IR-sensitive camcorder and Redlake camera were controlled by a PC laptop and desktop, respectively, in a partitioned side of the experimental room to remove potential visual cues from the LCD monitors (room

illuminance <0.015 cd m⁻²). In addition, a black Plexiglas sheet covered the lateral side of the flow tank to make certain that fish could not use any visual cues to aid in station holding relative to the cylinder. The black Plexiglas sheet was removed for the light experiments.

Experimental protocol

A Kármán vortex street was generated at a Reynolds number of 18 000 by placing a 5 cm, D-section cylinder in a uniform current of 42 cm s⁻¹ (or 2.5 *L* s⁻¹, where *L* is the total length of the fish). Experiments consisted of four treatments, intentionally conducted in the following non-random sequence: control fish possessing vision with a functional lateral line tested on day 1 (abbreviated V+L₊₁), fish without vision with a functional lateral line tested on day 1 (V–L₊₁), fish with vision without a functional lateral line on day 2 (V+L_{–2}), and fish without vision and a functional lateral line on day 2 (V–L_{–2}). Fish were first tested in the control treatment to confirm that they could Kármán gait as in previous studies (Liao et al., 2003a; Liao et al., 2003b). Paired light/dark treatments on trout with an intact lateral line (V+L₊₁ and V–L₊₁) were performed sequentially in the mid-afternoon of the first experimental day. Fish were then taken out of the flow tank and placed in a holding chamber overnight. Paired tests on trout with a blocked lateral line in the light and dark (V+L_{–2} and V–L_{–2}, respectively) were conducted the following day. The sequence of cobalt chloride treatment was not randomized because the recovery time after treatment with cobalt chloride varies from days to weeks (Karlsen and Sand, 1987; Montgomery et al., 1997). Testing fish with a blocked lateral line first would introduce variance in the start times of subsequent treatments and thus fish size, because of growth. Since Kármán gait kinematics and preference are most sensitive to the ratio of body length to cylinder diameter, significant growth would confound the results. One implicit assumption in these experiments is that fish with a blocked lateral line did not retain a spatial image of the relative position of the cylinder in the flow tank from the previous day. To test the assumption that fish do not alter swimming kinematics due to previous exposure to the experimental setup, the kinematics for control fish (*N*=4 fish) were collected on two successive days (V+L₊₁ and V+L₊₂) and compared. This is important when comparing experiments between fish with an intact lateral line (conducted on day 1) and cobalt-exposed fish (conducted on day 2), in which days of exposure to the experimental setup is a confounding factor. By controlling for prior experience to the experimental setup, kinematic comparisons made between treatments only reflect manipulation of light and the ability to sense flow with the lateral line. Similar to the V+L₊₁ fish, the V+L₊₂ fish were statistically compared to all other treatments.

Data analysis

The following kinematic variables were measured as in previous studies (Liao et al., 2003a; Liao et al., 2003b; Liao, 2004): lateral amplitude of the head, center of mass (COM), and tail tip relative to the body midline, maximum head angle

relative to the x axis (long axis of the flow tank), body wavelength, downstream distance from the cylinder, body wave speed, maximum curvature, and tail-beat frequency. The COM was determined *post-mortem* for each fish by iteratively balancing the body between right and left side pins. Body wavelength was obtained by dividing the wave speed (determined by tracking the maxima of each wave crest as it passed down the body) by the tail-beat frequency, where tail-beat frequency was calculated by averaging at least four consecutive tail-beats over a known time. A customized Matlab program was then used to plot the position of the head relative to the cylinder every five seconds for 1 h ($N=4$ fish) to assess the preference of fish to hold station in a vortex street. Fish were categorized as 'entraining' if the head was positioned in a predetermined rectangular region to either side and just downstream of the cylinder (each region was 7×15 cm), and as 'Kármán gaiting' if the head was positioned in a rectangular region centered 20 cm downstream of the cylinder (10×15 cm).

Statistical tests

The four treatments cannot be considered independent since the same individuals are used for each treatment. Therefore, paired *t*-tests were used to determine differences in the means of the various kinematic variables between treatments, where each mean value for each individual is the average of four tail-beats. Probability plots were generated for all datasets to test for the assumption of normality (not shown). Sequential Bonferroni corrections were performed to account for multiple paired tests and the alpha level adjusted accordingly at $\alpha=0.05$ (Rice, 1989). Means and standard errors were calculated for all variables. All statistical tests were performed in Systat version 9 for the PC.

Results

The effect of the lateral line and vision on Kármán gait kinematics

Compared to control fish, which had vision and an intact lateral line (Fig. 1A), fish treated with cobalt chloride to block the lateral line (Fig. 1B) displayed a significantly decreased ability to escape from a sudden jet of water, as measured by distance traveled by the head over a known period of time. After the end of each 2-day experiment, consisting of the four sequential treatments, fish were tested again to confirm that the lateral line was still blocked (Fig. 1C).

Kármán gaiting trout in the control treatment adopted a tail-beat frequency similar to the vortex shedding frequency of the cylinder and a body wavelength that was longer than the wake

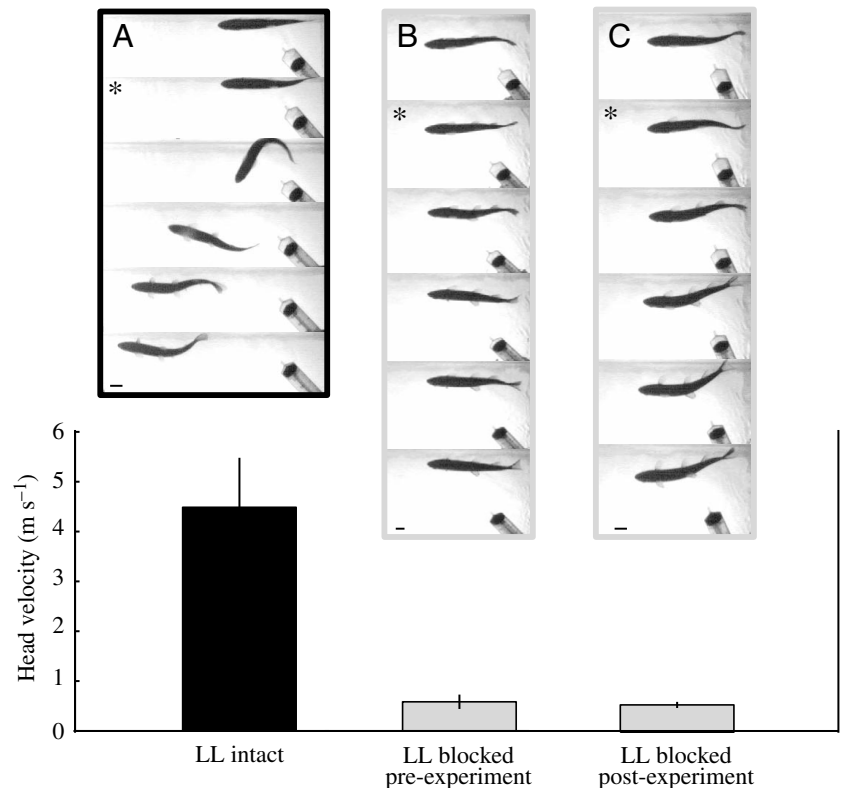
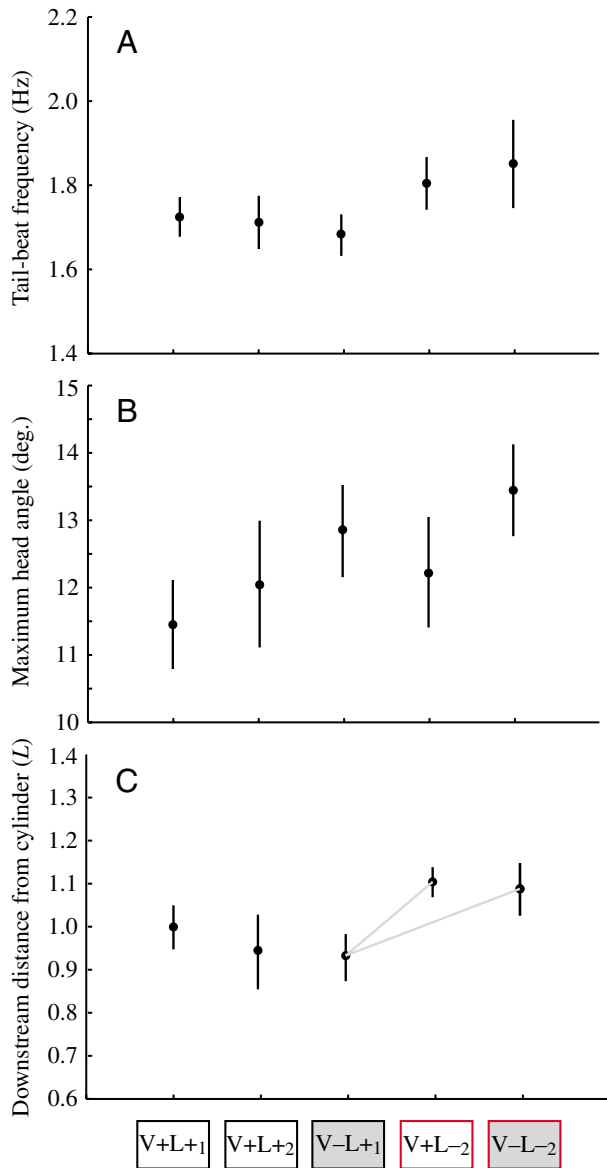


Fig. 1. Successive ventral view images (100 ms apart) of a trout with an intact lateral line (A), showing an escape response to a sudden jet of water directed at the body from a syringe (asterisk indicates the start of the jet). Images correspond to the black bar on the graph of head velocity shown below ('LL intact'). When the same trout is treated with cobalt chloride to block the lateral line it no longer exhibits an escape response to a jet of water (B, gray bar, 'LL blocked pre-experiment'). After the experiment, fish were retested to confirm that the cobalt chloride treatment did not wear off (C, 'LL blocked post-experiment'). Scale bars, 1 cm. All values are mean \pm s.e.m., $N=4$ fish.

wavelength, consistent with previous studies (Liao et al., 2003a; Liao et al., 2003b). Certain kinematic variables did not vary significantly regardless of whether vision and/or the lateral line was blocked. For example, average tail-beat frequency and maximum head angle was not statistically different across treatments (Fig. 2A,B; $P>0.43$, $N=16$ tail-beats for four fish; Table 1). Note that these values are relatively similar in pattern but lower than for previous studies where the fish length was lower and the current velocity was higher (Liao et al., 2003b).

Blocking the lateral line altered all other Kármán gait kinematic variables measured, compared to trout with an intact lateral line. Trout with a blocked lateral line Kármán gait further downstream relative to the cylinder than trout with an intact lateral line, regardless of whether the experiment is performed in the light or the dark, though this difference is only significant in the dark (Fig. 2C; $P<0.009$, $N=16$ tail-beats for four fish). Kármán gaiting trout with a blocked lateral line in the dark adopted a longer and more variable body wavelength than day 1 control fish (Fig. 3A; 2.19 ± 0.2 vs $1.71 \pm 0.04 L$, $P<0.002$, $N=16$ tail-beats for four fish). Note that standard error is shown but standard deviation, the true measure of variance,



exhibits the same relative relationship since sample sizes are equal for all treatments. A blocked lateral line also caused the body wave to travel faster towards the tail (Fig. 3B; $3.80 \pm 0.2 L s^{-1}$ in the dark and $3.49 \pm 0.2 L s^{-1}$ in the light, vs 2.95 ± 0.06 for the day 1 control treatment, $P < 0.002$, $N = 16$ tail-beats for four fish). There were no differences in lateral head amplitude across treatments (Fig. 3C), but trout with a blocked lateral line displayed a significantly lower tail tip amplitude in the dark ($0.15 \pm 0.01 L$) than trout with an intact lateral line in the dark ($0.19 \pm 0.01 L$, $P < 0.04$, $N = 16$ tail-beats for four fish) and in the light ($0.19 \pm 0.01 L$, $P < 0.003$, $N = 16$ tail-beats for four fish). Lateral COM amplitude followed the same relationship of significance across treatments as the tail tip amplitude. Compared to control fish, maximum body curvatures were lower when both vision and lateral line were blocked (Fig. 4; $1.75 \pm 0.07 1/L$ in the day 1 control treatment vs $1.46 \pm 0.09 1/L$, $P < 0.03$, $N = 16$ tail-beats for four fish). In addition, fish with an intact lateral line in the dark have a significantly higher body

curvature than fish with a blocked lateral line in the light (Fig. 4; $1.92 \pm 0.07 1/L$ vs $1.43 \pm 0.11 1/L$, $P < 0.05$, $N = 16$ tail-beats for four fish).

Fig. 2. Tail-beat frequency, maximum head angle and downstream head distance from the cylinder for all treatments. The x axis (from left to right): experiments in the light with lateral line intact for the first day of cylinder exposure ($V+L+1$); the same experiments with fish exposed to the cylinder on two consecutive days ($V+L+2$, see Materials and methods); experiments in the dark (gray fill) with lateral line intact on the first day ($V-L+1$); experiments in the light with lateral line blocked on the second day (red box, $V+L-2$); and experiments in the dark with lateral line blocked on the second day (gray fill and red box, $V-L-2$). Gray lines connect treatments that are statistically significant at $P < 0.05$. Values for control fish that were exposed to the cylinder for one ($V+L+1$) and two consecutive days ($V+L+2$) are statistically the same, illustrating that fish do not alter swimming kinematics as a result of previous exposure to the experimental setup. By controlling for prior experience to the experimental setup, kinematic comparisons made between treatments reflect the presence/absence of visible light and the ability to sense flow with the lateral line. (A) Tail-beat frequency does not differ significantly across treatments, though there is a tendency for fish with a blocked lateral line to exhibit slightly higher tail-beat frequencies and variability. (B) Maximum head angles do not differ significantly across treatments, but fish in the dark tend to exhibit slightly larger head angles regardless of lateral line functionality. (C) Fish with a blocked lateral line hold station further downstream from the cylinder than fish with an intact lateral line in the dark, where station-holding is measured as the distance from the tip of the snout to the downstream edge of the cylinder (where L is the total length of the fish). Within lateral line treatments, there is a tendency for fish in the dark to hold station further downstream from the cylinder. All values are mean \pm s.e.m., $N = 16$ tail-beats for four fish.

curvature than fish with a blocked lateral line in the light (Fig. 4; $1.92 \pm 0.07 1/L$ vs $1.43 \pm 0.11 1/L$, $P < 0.05$, $N = 16$ tail-beats for four fish).

The effects of vision and the lateral line on the preference for trout to Kármán gait or entrain

Trout showed a preference for holding station at different hydrodynamic locations around the cylinder, either entraining or Kármán gaiting (Fig. 5A,B), depending on which sensory cues were available. The lack of a regular pattern of axial undulation during entraining (Fig. 5A) differs dramatically from the large amplitude body motions seen during Kármán gaiting (Fig. 5B). In the light, trout with a functional lateral line (Fig. 6A; $V+L+1$) spent the majority of time Kármán gaiting whereas in the dark trout preferred to entrain (Fig. 6B; $V-L+1$). When the lateral line was blocked, fish in the light would still Kármán gait (Fig. 6C; $V+L-2$). Note the variation in behavior across individuals; some of these fish entrained (Fig. 6C, orange and green circles). Blocking vision and the lateral line (Fig. 6D; $V-L-2$) caused all fish to entrain. Thus, regardless of lateral line functionality, in the absence of light fish prefer to entrain over Kármán gaiting. When data from all fish are pooled together (Fig. 7), the proportion of time spent Kármán gaiting in the light was larger for fish with an intact lateral line ($V+L+1$; 50 out of 60 min, or 83% of the experiment duration) than for those with a blocked lateral line ($V+L-2$; 25 out of 60 min, or 41% of the experiment duration). The overall pattern

Table 1. *Kármán gait kinematic variables across experimental treatments*

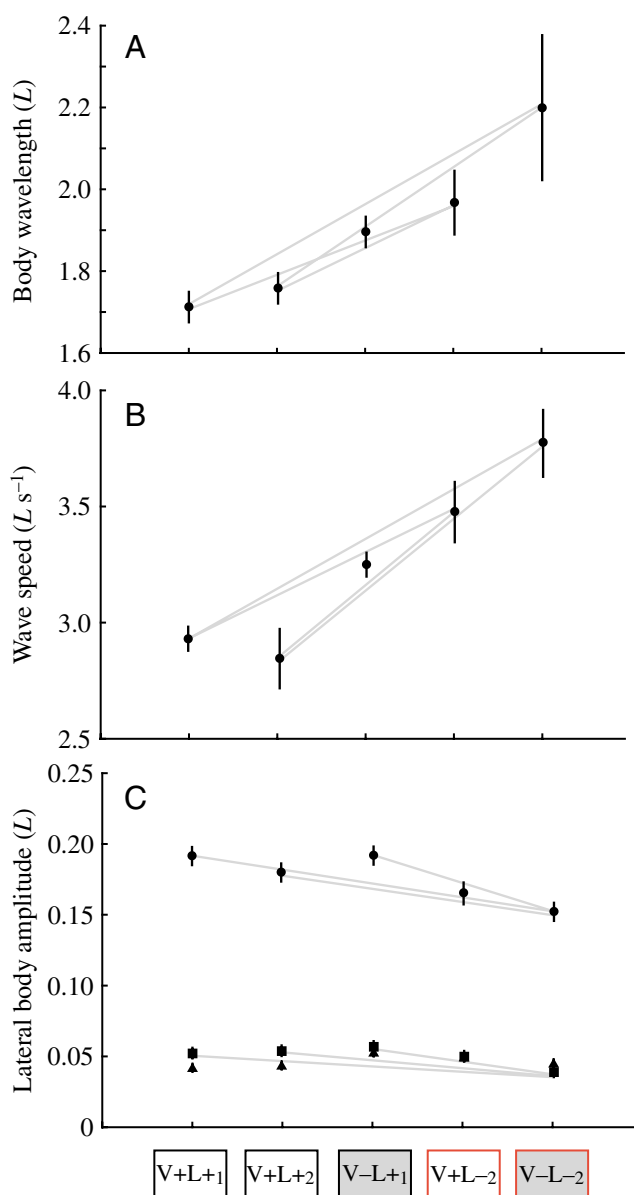
| Variables | V+L+ ₁ | V-L+ ₁ | V+L- ₂ | V-L- ₂ |
|-------------------------------|-------------------|-------------------|-------------------|-------------------|
| Tail-beat frequency (Hz) | 1.73±0.05 | 1.67±0.04 | 1.80±0.07 | 1.85±0.11 |
| Max. head angle (degrees) | 11.46±0.01 | 12.90±0.01 | 12.21±0.01 | 13.47±0.01 |
| Cylinder distance (L) | 1.02±0.05 | 0.90±0.05 | 1.11±0.03 | 1.07±0.06 |
| Body wavelength (L) | 1.71±0.04 | 1.90±0.04 | 1.94±0.09 | 2.19±0.2 |
| Wave speed ($L s^{-1}$) | 2.95±0.06 | 3.25±0.06 | 3.49±0.2 | 3.80±0.2 |
| Head amplitude (L) | 0.04±0.01 | 0.05±0.01 | 0.05±0.01 | 0.04±0.01 |
| COM amplitude (L) | 0.05±0.01 | 0.06±0.01 | 0.05±0.01 | 0.04±0.01 |
| Tail tip amplitude (L) | 0.19±0.01 | 0.19±0.01 | 0.16±0.01 | 0.15±0.01 |
| Max. body curvature ($1/L$) | 1.75±0.07 | 1.92±0.07 | 1.43±0.11 | 1.46±0.09 |

V+, vision; V-, no vision; L+, lateral line intact; L-, lateral line blocked.

Subscripts denote day of exposure to the experimental setup.

Total body length (L)=16.6±0.4 cm, $N=4$ fish.

All values are means ± s.e.m., $N=16$ tail-beats.



is that trout will choose to Kármán gait whenever it is light. In the dark, fish prefer to entrain than to Kármán gait. This occurs both with (V-L+₁; 40 out of 60 min, or 67% of the experiment duration) and without (V-L-₂; 44 out of 60 min, or 73% of the experiment duration) a functional lateral line (Fig. 7). Trout with both vision and an intact lateral line (Fig. 8A; V+L+₁) begin to Kármán gait in the vortex street quickly after being introduced to the flow tank for the first time. This ability to initiate and maintain Kármán gating behavior is diminished when the experiment is performed in the dark (Fig. 8B; V-L+₁). For example, fish start Kármán gaing at the beginning of the experiment but then change to entraining at various times. When the lateral line is blocked, fish with vision will divide their time more equally between Kármán gaing

Fig. 3. Body wavelength, body wave speed, and lateral amplitude along the body for all treatments, where L is the total length of the fish. The x axis (from left to right): experiments in the light with lateral line intact for the first day of cylinder exposure (V+L+₁); the same experiments with fish exposed to the cylinder on two consecutive days (V+L+₂, see Materials and methods); experiments in the dark (gray fill) with lateral line intact on the first day (V-L+₁); experiments in the light with lateral line blocked on the second day (red box, V+L-₂); and experiments in the dark with lateral line blocked on the second day (gray fill and red box, V-L-₂). Gray lines connect treatments that are statistically significant at $P<0.05$. Values for control fish that were exposed to the cylinder for one (V+L+₁) and two consecutive days (V+L+₂) are statistically the same, illustrating that fish do not alter swimming kinematics as a result of previous exposure to the experimental setup. (A) Body wavelength and (B) speed of propagation down the body are statistically higher when the lateral line is blocked and tend to increase in magnitude and variance in the dark. (C) Lateral body amplitudes were measured relative to the midline at three locations. Circles represent the tail tip, squares represent the center of mass (COM), and triangles represent the snout. The tail tip and COM amplitudes for fish in the dark with a blocked lateral line (V-L-₂) are significantly lower than control fish on day 1 (V+L+₁) and 2 (V+L+₂), as well as for fish in the dark with an intact lateral line (V-L+₁). All values are mean ± s.e.m., $N=16$ tail-beats for four fish.

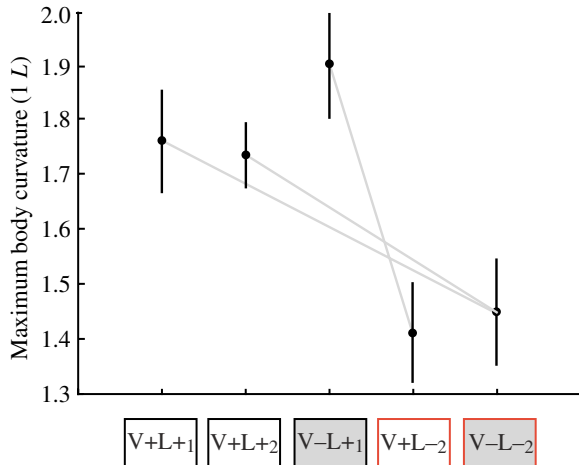


Fig. 4. Fish with a blocked lateral line have a lower maximum body curvature than fish with an intact lateral line. The x axis (from left to right): experiments in the light with lateral line intact for the first day of cylinder exposure ($V+L+1$); the same experiments with fish exposed to the cylinder on two consecutive days ($V+L+2$, see Materials and methods); experiments in the dark (gray fill) with lateral line intact on the first day ($V-L+1$); experiments in the light with lateral line blocked on the second day (red box, $V+L-2$); and experiments in the dark with lateral line blocked on the second day (gray fill and red box, $V-L-2$). Gray lines connect treatments that are significant at $P < 0.05$. Values for control fish that were exposed to the cylinder for one ($V+L+1$) and two consecutive days ($V+L+2$) are statistically the same, illustrating that fish do not alter swimming kinematics as a result of previous exposure to the experimental setup. All values reported are mean \pm s.e.m., $N=16$ tail-beats for four fish, where L is the total length of the fish.

and entraining (Fig. 8C; $V+L-2$). When both vision and the lateral line are blocked (Fig. 8D; $V-L-2$), fish predominately entrain but occasionally explore other regions of the flow tank, including Kármán gaiting in the vortex street. Entraining fish with an intact lateral line showed a tendency to alternate between right and left sides of the cylinder (Fig. 9A), whereas the same fish entraining with a blocked lateral line tended to remain on one side of the cylinder for the entire experiment (Fig. 9B).

Discussion

This study addresses two questions related to fish swimming in turbulent environments. The first question investigates how vision and the lateral line play a role in Kármán gaiting kinematics. The second question deals with how these two sensory modalities affect the preference to associate with environmental vortices when fish are given several hydrodynamic habitats to choose from. Thus, just because an animal is able to perform a behavior does not mean that it prefers to perform the behavior. Trout in this study display the ability to Kármán gait in all experimental treatments, but the preference to Kármán gait, as indicated by a larger proportion of time spent holding station in the vortex street *versus* other

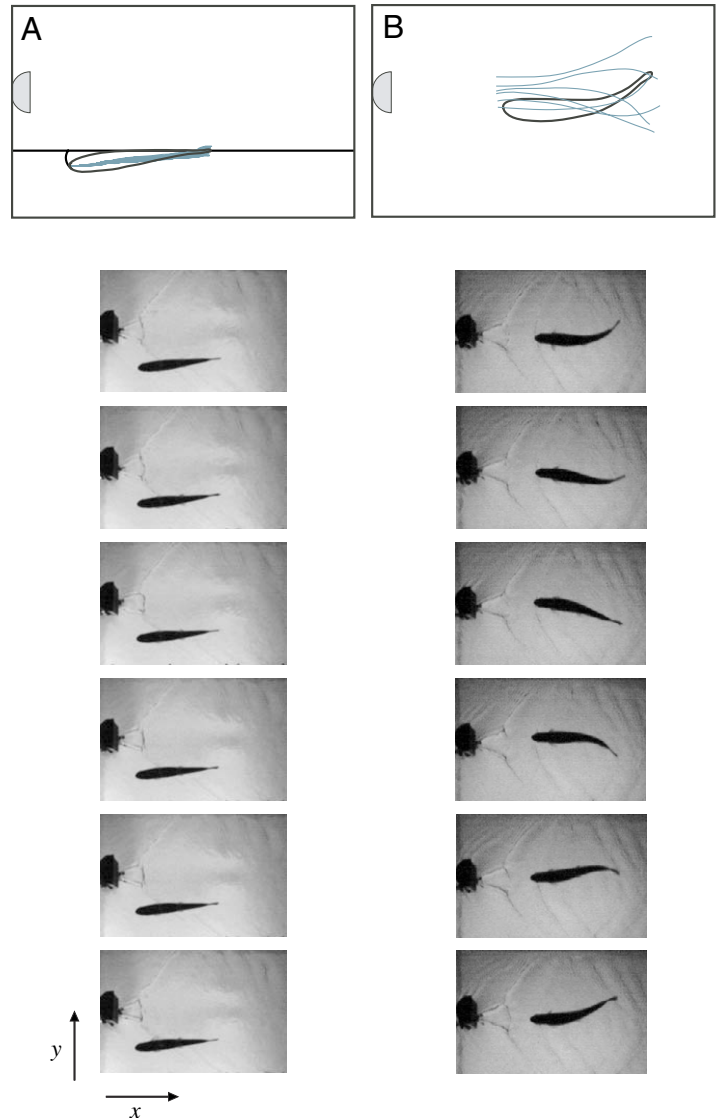


Fig. 5. Digitized silhouette and midlines of a trout (A) entraining and (B) Kármán gaiting around a 5 cm D-section cylinder, along with corresponding ventral view images, from top to bottom (100 ms apart). Flow is from left to right at $2.5 L s^{-1}$, where L is total body length. Note that during entraining the body axis is tilted at an angle to the x axis. Midlines of entraining fish demonstrate the lack of axial undulation, in contrast to the large amplitude body undulations seen in Kármán gaiting fish.

hydrodynamic environments, varied drastically across treatments. The first question addresses the biomechanical effect of sensory ablation on vortex capture and will be discussed below, whereas the second question addresses the topic of behavioral choice and will be treated in subsequent sections.

The relative roles of vision and lateral line feedback on the kinematics of the Kármán gait

What roles do vision and the lateral line play in the ability to exploit vortices in a cylinder wake? This question is further

complicated given that, for short periods of time, no sensory feedback is needed for a fish to move against the downstream flow in an oscillating vortex street. Theoretically, the hydrodynamic conditions of an oscillating wake make it possible for any foil-shaped object of the appropriate size to generate thrust passively (Bose and Lien, 1990; Wu and Chwang, 1975). Experimental evidence shows that a dead trout towed behind a cylinder can momentarily synchronize its body kinematics to the oscillating flow of a vortex street to generate thrust (Beal et al., 2006; Liao, 2004). Passive thrust generation to hold station or move upstream relative to the earth frame of

reference is a transient phenomenon because vortex streets are inherently turbulent. For a fish to remain in the cylinder wake for sustained periods requires sensory feedback from vision or the lateral line to facilitate body and fin control.

Fishes rely on both visual (Ingle, 1971; Roeser and Baier, 2003) and hydrodynamic (Coombs et al., 2001; Dijkgraaf, 1963; Engelmann et al., 2000) cues to adapt their swimming movements to their immediate environment. Kármán gait kinematics change when the lateral line is blocked, indicating that hydrodynamic feedback is used to alter motor output accordingly in turbulent flows. The greater variability in body

wavelength for trout with a blocked *versus* intact lateral line underscores the importance of detecting local flow along the body in adjusting Kármán gait kinematics to maintain a favorable posture to facilitate vortex capture. In addition, trout with a blocked lateral line hold station further downstream from the cylinder than fish with an intact lateral line. These findings demonstrate that at least some proportion of Kármán gait kinematics are under active control and they are not the sole result of passive buffeting of the body by vortices. Longer body wavelength and faster wave speed suggest that Kármán gaiting is less efficient or more energetically costly without a functional lateral line. The fact that trout in the light with a blocked lateral line do not spend as much time Kármán gaiting as trout with a functional lateral line (Fig. 7) provides behavioral evidence in support of this hypothesis. Whether altered Kármán gait kinematics reflect muscle activity and changes in energy expenditure for the individual is currently not known. When lateral line functionality is held constant (i.e. within fish with an intact or blocked lateral line), the presence or absence of light does not change Kármán gait kinematics. This provides further evidence that when trout hold station in a vortex street the lateral line, rather than vision, plays a larger role in body kinematics.

One exception occurs where vision alone can alter Kármán gait kinematics. Fish with a blocked lateral line in the dark have a greater variability in body wavelength than fish in the light. These fish seem to have more difficulty exploiting vortices, often drifting position within the vortex street, displaying ‘corrective’ motions, or switching to traditional undulatory swimming such as seen in uniform flow. Vision allows fish to maintain a consistent position relative to the cylinder. This may minimize the exposure to flow variation and thus variation in body wavelength, since the predictability and energy of the vortices decreases with downstream distance from the cylinder.

Applications of vortex capture in swimming fishes

This study investigates how the lateral line affects

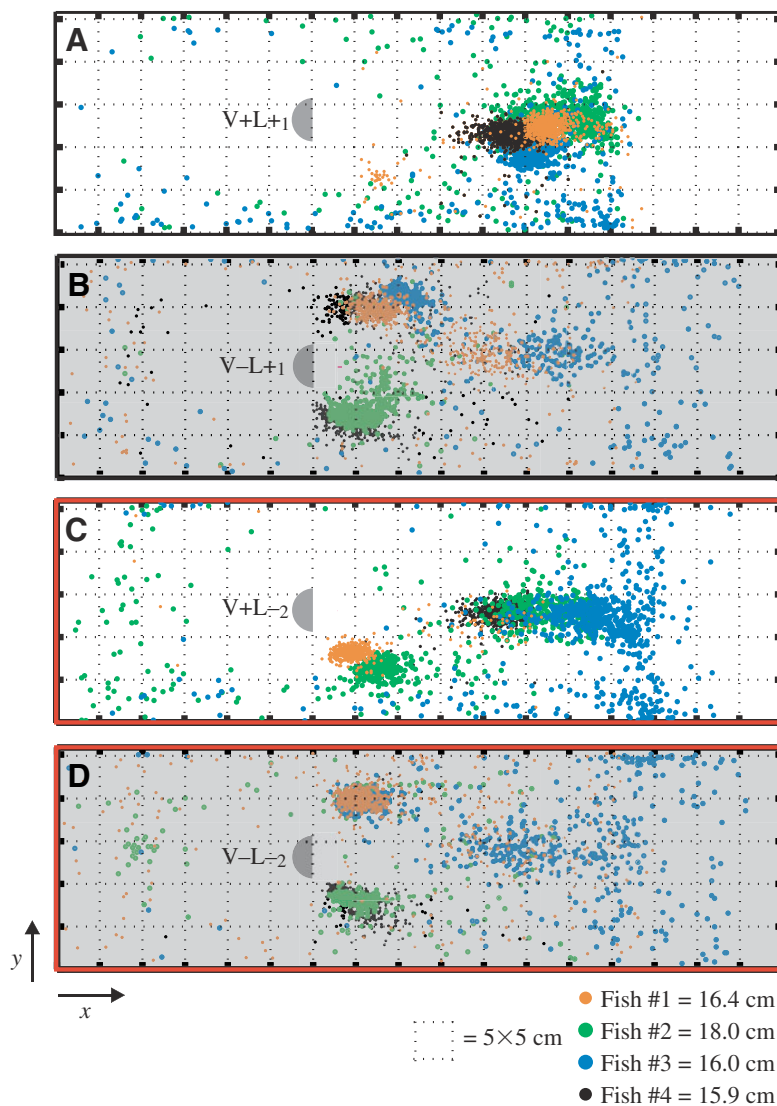


Fig. 6. Head location in the flow tank every 5 sec for 1 h (720 data points per fish), where each color represents an individual ($N=4$ fish). From top to bottom; (A) treatment in the light with lateral line intact ($V+L_{+1}$), (B) treatment in the dark with lateral line intact ($V-L_{+1}$, gray fill), (C) treatment in the light with lateral line blocked ($V+L_{-2}$, red box), and (D) treatment in the dark with lateral line blocked ($V-L_{-2}$, gray fill and red box). Fish in the light prefer to Kármán gait (A), even in the absence of a functional lateral line (C). Fish in the dark (B,D) prefer to entrain regardless of lateral line functionality. Total body lengths of individual fish are given.

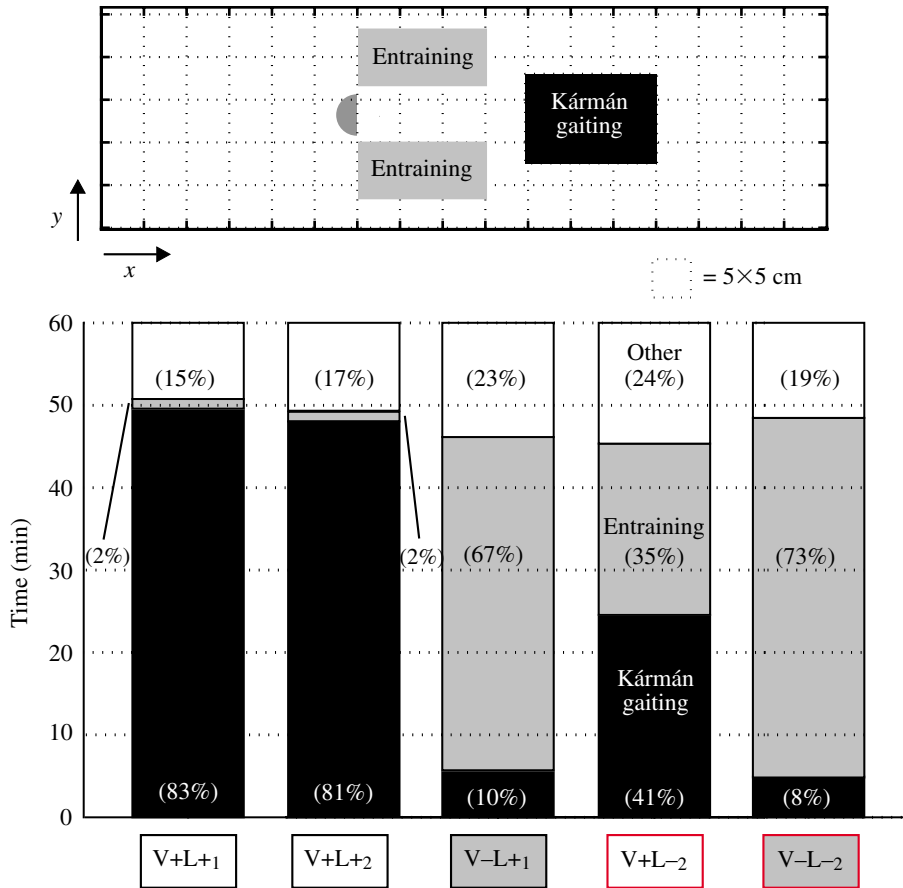


Fig. 7. Regions around a cylinder in flow that trout will either entrain (defined as two rectangular regions on either side of the cylinder, 7×15 cm) or Kármán gait (defined as a single rectangle centered along the midline of the cylinder wake, 10×15 cm). In the light, fish prefer to Kármán gait in the vortex street downstream from the cylinder (black fill) for the majority of the time during a 60-min experiment, especially when the lateral line is intact (V+L+1). Values for fish in the light with an intact lateral line exposed to the cylinder for two consecutive days (V+L+2) are almost identical to those exposed for 1 day (V+L+1), indicating that previous experience in the flow tank does not alter the preference to Kármán gait. In contrast to their reaction in the light, fish in the dark do not spend much time in the vortex street regardless of lateral line functionality (V-L+1 or V-L-2), preferring to entrain (gray fill) just downstream and to the side of the cylinder. The time that fish spent exploring other regions of the flow tank (white) is similar across treatments.

the ability to use environmental vortices to benefit swimming performance. Similarly, the ability of a swimming fish to sense and presumably control self-generated vortices from its undulating body could increase swimming efficiency. To test the hypothesis that detection of self-generated vortices plays a role in steady swimming kinematics, one would need to compare swimming behavior of fish with and without a blocked lateral line. When Dijkgraaf (Dijkgraaf, 1963) performed such experiments he found that lateral line ablation did not cause gross differences in the swimming performance of cyprinids in uniform current if visual cues existed, indicating that the motions of steady swimming are feedforward and can proceed in the absence of hydrodynamic feedback. Strouhal number, a metric for swimming efficiency that uses tail-beat frequency, also does not deviate in the absence of a functional lateral line (S. Coombs, personal communication). Another line of evidence comes from the preservation of a stereotypical swimming motor pattern in paralyzed preparations of undulatory aquatic vertebrates, in which no self-generated hydrodynamic stimuli can exist (Grillner, 1985; Sillar and Roberts, 1988). Presumably the ability to sense body-bound vortices is not necessary to establish the gross motor pattern of swimming, but in the absence of detailed kinematics and physiological measurements the role of the lateral line in affecting undulatory efficiency cannot be ruled out. Based on the available experimental data, a blocked lateral line

noticeably alters swimming kinematics in turbulent but not uniform flow. Though both Kármán gaiting and steady swimming involve body–vortex interactions the vortices in each situation can differ in size and strength. Vortices generated by the body during swimming are probably smaller and weaker than cylinder-generated vortices used in this study, and as such may not be easily detected or even ignored by the lateral line. The ability to cancel self-generated noise in order to be sensitive to biologically important signals from the environment has been well documented for the lateral line and other modalities (Bell, 2001; New and Bodznick, 1990). It is possible that fish are able to anticipate the progression of self-generated vortices down the body but that this information is not translated into a change in swimming motor output unless there is a strong enough flow perturbation to warrant a kinematic response. In light of these previous studies we can understand why the general pattern of axial undulation during steady swimming does not depend on hydrodynamic feedback, especially if visual cues are available to use to hold station in the earth frame of reference.

The cylinder vortices used in this study are larger and stronger than body-generated vortices during steady swimming (Nauen and Lauder, 2002). Cylinder vortices cause deviations from steady swimming motions because they may be more readily detected and elicit a motor response. Direct recordings from the lateral line nerve indeed show a sensitivity

to environmental vortices (Chagnaud et al., 2006). However, electromyography data reveal that these signals may not translate into muscle activity along most of the body (Liao, 2004). Alternatively, vortices that have enough momentum to move the fish relative to the earth frame of reference can cause changes in swimming motions. This can occur independently from hydrodynamic sensing by the lateral line, as seen when a dead fish is towed behind a cylinder (Liao, 2004). In the case of this study, Kármán gaiting involves a combination of active and passive mechanisms. The lateral line is probably involved in relaying selected information from the vortex street to guide active body and fin movements, since kinematic changes only occur when the lateral line is blocked. Since turbulent flows can destabilize swimming trajectories and increase the cost of locomotion, the ability to sense vortices is probably at a

premium (Enders et al., 2003; Pavlov et al., 2000; Webb, 2004).

To Kármán gait or not to Kármán gait?

When trout hold position in a vortex street their body kinematics are more influenced by blocking the lateral line than by blocking vision. But how do these sensory modalities affect the *decision* to hold station in a vortex street instead of other regions around a cylinder? Trout will Kármán gait when visual cues are available, independent of whether or not the lateral line is intact or blocked (Figs 6–8). This suggests that fish can Kármán gait using vision alone. Indeed, Dijkgraaf (Dijkgraaf, 1963) observed early on that “the visual system appears to be the most likely sensory channel to provide fish with a reference point as an indicator of body displacement.” He found that given visual cues the presence or absence of a functional lateral line made no difference in the ability to display a rheotactic response. Much like fish swimming in steady flows, fish predominantly use vision to orient themselves in unsteady currents in the wake of bluff bodies. In the case of this study, trout are visually orienting to the cylinder in order to hold station at a consistent downstream region of the vortex street. It is unlikely that trout visually detected vortices since the water did not contain obvious particulate matter or air bubbles.

In the dark, trout do not choose to spend much time in the vortex street, even when they possess an intact lateral line. Thus, a functional lateral line alone does not enable fish to exploit the vortex street. The lateral line seems to promote the tendency to explore the surrounding hydrodynamic environment, perhaps to find a global rather than local region of favorable flow. Presumably, the feedback control required to maintain position in a turbulent vortex street requires more than just the ability to sense and respond to flows from moment to moment. These data suggest that vision is more influential than the lateral line in determining the preference to associate

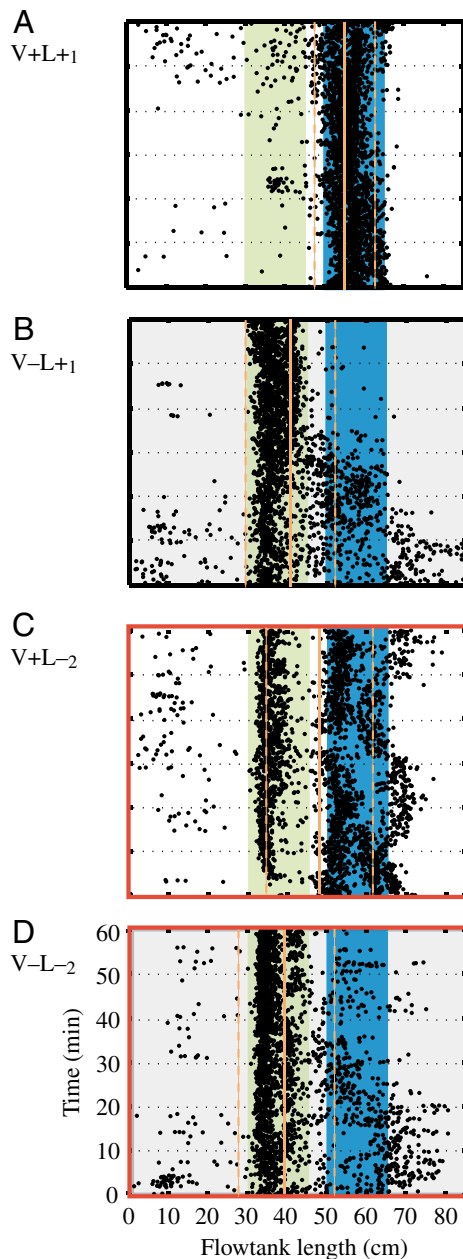


Fig. 8. Downstream position of the head in the flow tank every 5 s for 1 h under different experimental treatments ($N=4$ fish). (A) Fish that possess both vision and the lateral line ($V+L+1$) immediately start to Kármán gait in the vortex street at a defined distance downstream of the cylinder (blue shaded bar) and remain there for the entire experiment. Mean downstream positions are shown (vertical, orange solid line; $N=4$ fish) along with the standard deviation (orange broken lines). The green shaded bar indicates the region that fish occupy when they entrain. Note that the upstream edge of this region (30 cm) is where the downstream edge of the D-cylinder (not shown) is located. (B) In the dark (gray fill), fish with only a lateral line ($V-L+1$) initially explore the length of the flow tank and occasionally Kármán gait. However, by the last half of the experiment, all fish prefer to entrain. (C) In the light, fish with a blocked lateral line (red box; $V+L-2$) show both entraining and Kármán gaiting behavior without a dominating preference for either, unlike all other treatments. (D) Fish without vision or an intact lateral line (gray fill and red box; $V-L-2$), prefer to entrain rather than Kármán gait, much like in B. When fish with a blocked lateral line stray away from ‘entraining’ and ‘Kármán gaiting’ regions they do so throughout the experiment, unlike fish with an intact lateral line.

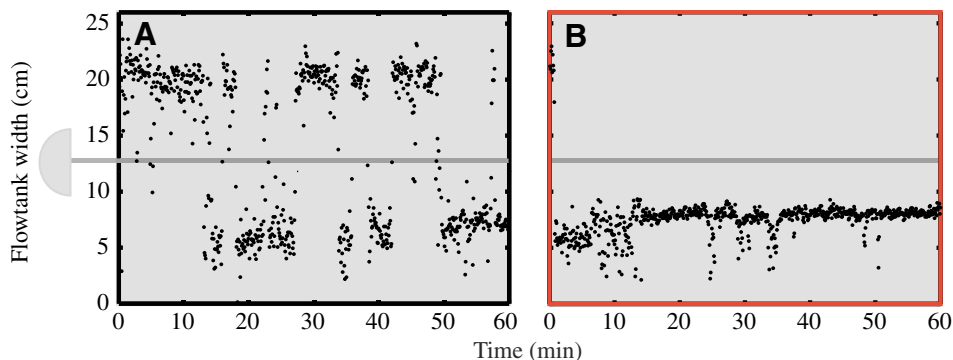


Fig. 9. Downstream position of the head every 5 s for 1 h for an individual trout, illustrating the role of the lateral line in facilitating exploration of the flow tank. (A; gray fill) In the dark, a fish with an intact lateral line alternately entrains between right and left sides of a cylinder. (B; gray fill with red box) When the lateral line is blocked, the same fish will continue to entrain in the suction region but no longer explores the other side of the cylinder. In the dark, fish do not prefer to Kármán gait in the vortex street.

with a vortex street (Fig. 7). In reality, trout probably depend on both the lateral line and vision to Kármán gait.

Entraining near the suction zone

The initial goal of this study was to investigate the effects of sensory input on the kinematics of Kármán gaiting. However, during the course of the experiments fish in the dark displayed a general avoidance of the vortex street, instead choosing to entrain close to the cylinder. Entrainment takes advantage of the low pressure suction region that forms immediately behind a cylinder in flow and extends approximately two cylinder diameters downstream from the cylinder (Zdravkovich, 1997). Studies have previously documented entraining for several species (Montgomery et al., 2003; Sutterlin and Waddy, 1975; Webb, 1998). Note that these studies did not document Kármán gaiting. This is most likely because they used lower flow velocities and smaller diameter cylinders, thus effectively giving fish the option only to entrain. Since the flow velocity and ratio of cylinder diameter to fish length are the key factors in eliciting the Kármán gait, altering these variables will alter the pattern of the shed vortices and subsequently affect the position fish adopt around a cylinder. The reason why trout in this study entrained almost exclusively in the dark and not in the light is not known, but may have to do with factors unrelated to hydrodynamics, which will be explored in a subsequent section.

Previous studies have shown that both the canal and superficial neuromasts of the lateral line system are required for obstacle entrainment (Montgomery et al., 2003; Sutterlin and Waddy, 1975), and that selective ablation of either neuromast type results in fish spending less time entraining. Sutterlin and Waddy (Sutterlin and Waddy, 1975) viewed the suction region as a discontinuity with the downstream flow and hypothesized that trout were able to hold station by using the posterior lateral line to detect this flow difference along the body. In support of this hypothesis trout in this study show no rhythmic body undulations when entraining, holding the body straight and at an angle (approximately 15° relative to the x axis; Fig. 5A) and correcting for perturbations by using their

fins. The lack of body undulation could also serve to minimize self-generated hydrodynamic noise. This explanation implies that the body of the trout is sampling the pressure difference across its body to maintain position relative to the cylinder. If this is the case then smaller fish that cannot span the suction region, and thus not detect the edges of flow discontinuity, should find it more difficult to entrain.

Future experiments could selectively block one neuromast type to assess its role in Kármán gaiting. Is there a division of function between neuromasts types as seen in other behaviors such as rheotaxis (Montgomery et al., 1997) and prey detection (Coombs et al., 2001)? Canal neuromasts have been shown to be able to detect local flows from a background of constant current velocity (Chagnaud et al., 2006; Engelmann et al., 2000). Thus, although the hydrodynamics of a cylinder wake has both velocity and acceleration components (Zdravkovich, 1997), the prediction is that acceleration-sensitive canal neuromasts would play a larger role in determining how fish alter Kármán gait kinematics (Coombs et al., 1989). Thus, species that have a relatively higher density of canal neuromasts should be more willing to swim in turbulent flows than species that have a higher density of superficial neuromasts (Engelmann et al., 2002).

Station holding without visual and hydrodynamic cues

In their natural habitat trout probably use multiple sensory modalities to hold station in turbulent flows. This paper shows that trout with vision but a blocked lateral line can still Kármán gait continuously, albeit with significantly different kinematics than control fish, illustrating how one sensory modality can compensate for the loss of another one to preserve a given behavior. Similarly, Dijkgraaf (Dijkgraaf, 1963) found that removal of the pars superior of the vestibular organ drastically affected swimming behavior, which after time was restored back to normal if fish possessed vision. One might predict that if trout in this study were given several weeks to allow compensation for an ablated sensory modality, the ability and preference to Kármán gait would be more similar across treatments.

This study demonstrates that fish can entrain even in the absence of hydrodynamic and visual cues, indicating that another mechanism must exist to explain how fish hold station near the suction region created by a bluff body. The most likely explanation is that fish may be using other sensory inputs besides vision and the lateral line to entrain. For example, sound cues generated by vortices shed from a cylinder, analogous to the vortex-induced Aeolian tunes generated when wind moves past telephone wires (Etkin et al., 1957), could be used to hold station relative to a cylinder. Alternatively, fish may be relying on the detection of flow-induced accelerations of the body. The suction region directly behind a cylinder is a simpler, less variable flow environment compared with the oscillating flow of a turbulent vortex street. Because of this, fish can entrain indefinitely without feedback from the lateral line or vision, unlike for Kármán gaiting. Although muscle spindles have not been identified in fish, presumably fish have the ability to sense whether they are contracting their muscles. Auditory cues, if additionally combined with the vestibular system and proprioceptive feedback from motor output, could provide sufficient information to maintain a constant spatial relationship with the cylinder in the absence of vision and the lateral line.

Entraining may exploit a passive mechanism for thrust generation such that the angled body acts as a lift-producing foil to serve a biomechanical rather than sensory function. The observation that the angled body posture is adopted even when fish cannot detect hydrodynamic stimuli lends support to this reasoning. To maintain in this position relative to the cylinder without body undulation, fish display frequent fin motions with no clear pattern of activity. In this way fish can maintain position relative to the cylinder by balancing the lift force that draws the body upstream with the drag force that pulls the body downstream. The mechanism underlying entraining has not been investigated and would benefit from quantitative flow visualization techniques.

Choosing to Kármán gait rather than entrain

Entraining probably requires minimal or no axial muscle activity given that the body does not undulate. Therefore, entraining is a potentially less energetically costly behavior than Kármán gaiting. Why then, do trout not choose to entrain all the time, for instance during light treatments? One possible reason is that entraining may be potentially less costly to perform but the penalty for losing position is greater than that for Kármán gaiting in a vortex street. Although this may not occur in the controlled conditions of the laboratory, flows in nature are invariably unpredictable and span orders of magnitude. Upon being displaced from the 'entraining' region into the fast surrounding flow outside of the cylinder wake, trout quickly respond by accelerating upstream to reestablish position. This burst of swimming would certainly involve red, and potentially white, axial muscle activity along the entire body.

Entraining fish with an intact lateral line voluntarily alternate between left and right sides of the cylinder (Fig. 9), which may

prevent fatigue on one side of the body, given the asymmetrical posture of entraining fish relative to the downstream flow axis. By contrast, entraining fish with a blocked lateral line tend to have fidelity to one side of the cylinder and do not tend to switch from one side to the other. This could reflect the ability of the lateral line to promote the exploration of the hydrodynamic environment. Fish with an intact lateral line may be searching for a globally favorable flow environment, whereas fish with a blocked lateral line must settle for a locally favorable environment. This hypothesis assumes that volitionally alternating position between the two sides of the cylinder (e.g. transitioning across the suction region) is less costly than being displaced downstream from the 'entraining' region.

Interestingly, fish displaced from entraining were rarely observed to transition to the Kármán gait. In contrast to entraining, Kármán gaiting may be less energetically costly to resume if the fish becomes displaced. Behavioral evidence supports this hypothesis. Kármán gaiting fish commonly leave the vortex street to intercept food only to immediately return to the same position. Since fish move largely passively with the lateral component of the oscillatory flow in a vortex street (Liao, 2004), resuming the Kármán gait would not require the sequential muscle contraction seen in propulsive, undulatory swimming. Rather, minimal red muscle activity may be needed to resume synchronization with the vortices, since the low-pressure vortices will inherently draw fish in. When Kármán gaiting fish drift too far downstream in the vortex street, they briefly switch to propulsive undulation to reestablish position in the vortex street. If fish play off vortices to resume position the metabolic investment may not be as large as during whole-body undulation during propulsive swimming in uniform flow, when no energy can be extracted from the environment (Beal et al., 2006). This is the case when entraining fish are displaced. If one does not assume that the penalty for displacement is higher for entraining than for Kármán gaiting and that energy savings was at a premium, one might expect that entraining, which requires no body undulation, might be the dominant behavior in all treatments. The fact that it is not suggests that factors beyond the physiology and mechanics of locomotion influence habitat selection. Measuring muscle activity and oxygen consumption would provide a basis to compare the energy savings entraining confers, if any, over Kármán gaiting or maintaining position in the bow wake in front of a cylinder (Liao et al., 2003b). Regardless of whether fish are Kármán gaiting or entraining, it is clear that in this study fish preferred to associate with vortical flows rather than uniform flow.

Future experiments may show that Kármán gaiting requires a larger energetic investment than entraining, based on the dramatic differences in body motions. Why then would fish prefer to Kármán gait rather than entrain in the light? One explanation could be that the decision to Kármán gait is related to feeding motivation. Trout are visual feeders that have been observed to intercept food readily while Kármán gaiting (Liao et al., 2003b). In the field, many fish swim and feed in turbulent flows more actively during the day than at night (Heggenes,

1988; Pavlov et al., 2000). Hungry fish have been documented to seek out turbulent flows whereas satiated fish prefer less complex flows (Pavlov et al., 2000), perhaps because turbulence can increase prey encounter rates (Lewis and Pedley, 2001; MacKenzie and Kiorboe, 1995) and enhance the success of these encounters by disorienting prey. The size of vortices required to promote Kármán gaiting are large enough to disorient favored prey such as small invertebrates, thus conveniently creating a foraging opportunity while facilitating reduced muscular activity (Liao, 2004). In addition, the side-to-side motion of the Kármán gait facilitates the ability to survey the environment and expands the range for prey detection and capture. Unless prey drifts directly towards an entraining fish, the cost to intercept it may be too high to warrant leaving the cylinder. The feeding hypothesis also explains why some trout Kármán gait while others do not (Fig. 6C, Fig. 8C). This hypothesis could be tested in future experiments by controlling for feeding motivation, which should lead to predictable outcomes of where fish position themselves around a cylinder in flow.

The results of this study offer insight into the contribution of the lateral line and vision to both the kinematics and hydrodynamic preference of freely swimming fish in the turbulent wake of a bluff body in flow. Both Kármán gaiting and entraining illustrate the ability to exploit vortical flows to hold station relative to the earth frame of reference rather than rely on active body undulation to generate thrust. In the light, Kármán gaiting is favored over entraining despite a potentially larger energetic cost. This suggests a general principle that is applicable to organisms moving freely in complex environments; control and physiological state, rather than energetic savings, can play a deciding role in habitat selection. The results of this paper provide quantitative progress towards an organismal understanding of sensorimotor control in turbulent environments.

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