

# Neuromuscular control of trout swimming in a vortex street: implications for energy economy during the Kármán gait

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## Summary

Approximating the complexity of natural locomotor conditions provides insight into the diversity of mechanisms that enable animals to successfully navigate through their environment. When exposed to vortices shed from a cylinder, fishes hold station by adopting a mode of locomotion called the Kármán gait, whereby the body of the fish displays large, lateral oscillations and the tail-beat frequency matches the vortex shedding frequency of the cylinder. Although field studies indicate that fishes often prefer turbulent flows over uniform currents, the effect of hydrodynamic perturbations on the mechanics, control and energetics of locomotion is still poorly understood. In this study, electromyography is used to measure red and white axial muscle activity for rainbow trout (*Oncorhynchus mykiss*) holding station in a vortex street. When trout Kármán gait, they show a significantly reduced but still rhythmic pattern of muscle activity compared with that seen when they swim steadily in uniform flow. Specifically, trout selectively activated only their anterior red axial muscles and abandoned the antero-posterior wave of red muscle activity that drives undulatory locomotion in uniform flow. This supports a previously proposed hypothesis that trout are not just swimming in the reduced flow behind a cylinder (drafting). Anterior axial muscle activity was correlated to head amplitude during steady swimming but not during

the Kármán gait, indicating that while activation of muscles during the Kármán gait may aid in stability and control, vortices determined overall head motion. Furthermore, anterior red axial muscle activity, the only region of muscle activity shared between both the Kármán gait and steady swimming, had a lower intensity and longer duration during the Kármán gait. At times when paired fins were active during the Kármán gait, there was no axial muscle activity measured, lending support to a passive mechanism of thrust generation in oscillating flows. Comparisons with dead trout towed behind a cylinder confirm this intriguing observation that live trout may temporarily adopt the Kármán gait with no axial muscle activity, revealing paradoxically that at times fish can passively move against turbulent flow. To Kármán gait for prolonged periods, however, trout must adapt to the demands of turbulence by eliciting a shift in neural control strategy. By decoupling motor output both down and across the body, the pattern of rhythmic Kármán gait muscle activity may reflect the entrainment of a central pattern generator to environmental vortices.

Key words: electromyography, Kármán gait, fish swimming, rainbow trout, *Oncorhynchus mykiss*, axial muscle activity, turbulence, vortices, neural control, central pattern generators.

## Introduction

Studies of fishes swimming with undulatory motions in uniform flow reveal a sequential, rostral-caudal pattern of axial red muscle activity that bends the body into a traveling wave, propelling the fish forward (Altringham and Ellerby, 1999; Gillis, 1998b; Grillner and Kashin, 1976; Hammond et al., 1998; Jayne and Lauder, 1994; Wardle et al., 1995). Yet both field and laboratory studies have shown that fishes often prefer to associate with turbulent flows generated from water flowing past inanimate objects (Fausch, 1993; Gerstner, 1998; Heggenes, 2002; Liao et al., 2003a; Webb, 1998) or by other fishes (Breder, 1965; Fish, 1991; Herskin and Steffensen, 1998; Pitcher et al., 1976). These vortical flows provide an energy-rich environment unavailable in uniform currents that

can be exploited by fishes to enhance swimming performance (Breder, 1965; Hinch and Rand, 2000; Liao et al., 2003b; Streitlien and Triantafyllou, 1996; Weihs, 1973). However, we currently have little understanding of how the environment affects the neuromuscular control of aquatic locomotion, unlike in terrestrial studies (Biewener and Gillis, 1999; Gillis, 1998a; Jindrich and Full, 2002; Roberts et al., 1997).

In a recent study, trout were shown to volitionally hold station in an experimentally generated vortex street by exhibiting a novel, rhythmic undulating motion termed the Kármán gait (Liao et al., 2003a). During the Kármán gait, tail-beat frequency consistently approaches the rate at which vortices are shed from the cylinder, and the body oscillates

laterally with a magnitude similar to the spacing of the vortices. This indicates a phase locking of the swimming kinematics to the vortex wake and thus a potentially passive mechanism of holding station in fast, turbulent flows. It was hypothesized that trout use a largely passive mechanism to generate thrust when positioned in the sinusoidal flow of a vortex street (Liao et al., 2003a).

Despite the substantial and widespread benefits of vortex energy capture for fish locomotion, there are still no quantitative data that address the diversity and extent to which vortices might affect muscle activity patterns in swimming fishes (but see Liao et al., 2003b). Like many types of locomotion in animals, swimming is a rhythmic motion that is under the control of central pattern generators (CPGs; e.g. Grillner, 1985; Grillner and Kashin, 1976). Although one useful definition of a CPG is that it can occur in the absence of feedback from the environment (Grillner, 1975), the importance of sensory stimuli on determining the final motor output pattern of CPGs in naturally behaving animals cannot be overstated (reviewed in Cohen, 1992). Isolated spinal preparations provide a powerful opportunity to understand the fundamental neural circuitry of locomotion, but at the cost of shifting the emphasis away from the adaptive aspect of movement that is the hallmark of natural animal behavior (Cohen, 1992). As an alternative, the present study attempts to approach the control of locomotion as a behavior at the organismal level. A novel motor pattern associated with the Kármán gait may thus provide a unique opportunity to examine sensory-driven motor output for freely behaving fishes swimming among environmental vortices.

Here, electromyography is used to quantify red and white axial muscle activity to test the hypothesis that rhythmic axial muscle activity pattern in Kármán gaiting fish differs from the rostro-caudal traveling wave of muscle activity typical of fishes swimming in uniform flow. The second hypothesis to be tested is that cylinder vortices rather than axial muscle activity dominate Kármán gait kinematics. Finally, the third hypothesis to be tested is that short bouts of Kármán gaiting can proceed at times without any muscle activity.

## 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-liter circular freshwater tank ( $15 \pm 1^\circ\text{C}$ , mean  $\pm$  S.E.M.) with constant flow and fed commercial trout pellets daily. Five trout were used in the experiment, with a total body length ( $L$ ) of  $16.6 \pm 0.3$  cm (mean  $\pm$  S.E.M.).

### Electrode construction

Electrodes were constructed by threading one end of a double-stranded, insulated, stainless steel wire (0.005 cm diameter; California Fine Wire Co., Grover Beach, CA, USA) through the barrel of a hypodermic needle (26 gauge 5/8). The

tips of the wire were then stripped of insulation and splayed apart by 0.5–1.0 mm. The two exposed tines were then rolled into a hook using fine, electronic micro-forceps and pulled snug against the needle tip for insertion (Loeb and Gans, 1986).

### Surgical procedures

Trout were anesthetized in a  $15 \pm 1^\circ\text{C}$ , 5-liter holding tank containing a solution of  $0.0654 \text{ g l}^{-1}$  tricaine methanesulfonate (MS-222; Finquel Inc., Argent Chemical Laboratories Inc., Redmond, WA, USA) buffered with potassium hydroxide. Fish became unresponsive to tactile stimuli within minutes and were transferred into a tray containing a maintenance solution of MS-222 ( $0.00327 \text{ g l}^{-1}$  at  $15 \pm 1^\circ\text{C}$ ). During surgery, the gills of the fish were regularly irrigated with a solution of dilute MS-222 and oxygenated water. Four electrodes were inserted into the superficial, axial red muscles along the left side of the fish (Fig. 1; R1,  $0.23 L$ ; R2,  $0.40 L$ ; R3,  $0.56 L$ ; R4,  $0.73 L$ ). Two electrodes were also inserted into the white muscle, halfway

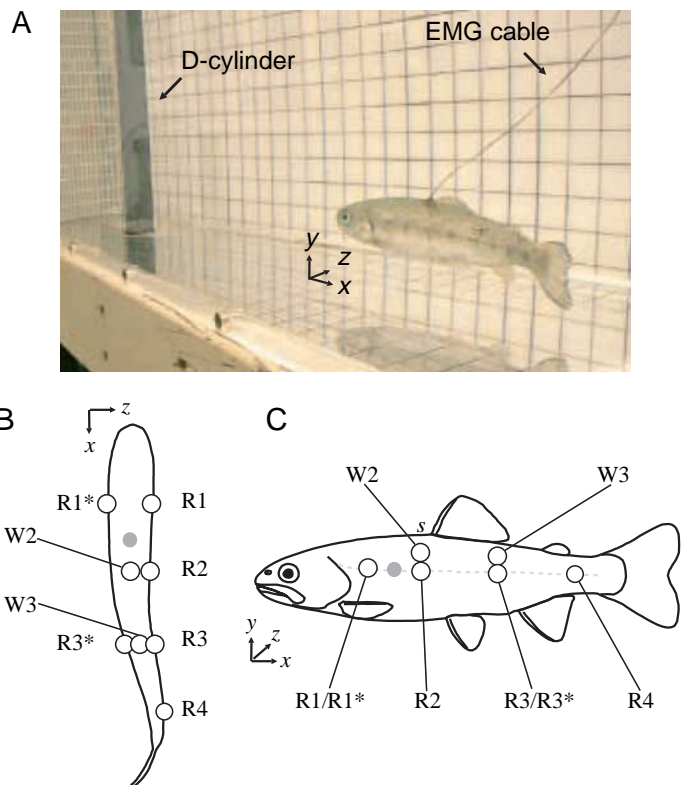


Fig. 1. (A) Posterolateral view of a trout Kármán gaiting behind a D-cylinder with fine wire electromyography electrodes inserted into the red and white axial muscles along the body (see Materials and methods for details). A map of electrode insertion sites for superficial red (R) and deep white (W) axial muscles along four longitudinal locations of the body in ventral (B) and lateral (C) view are shown. From the snout, insertion sites 1–4 correspond to 0.23, 0.40, 0.56 and  $0.73 L$  down the body from the snout, respectively, where  $L$  is total body length.  $s$  denotes the placement of a suture loop, used to hold individual electrode wires in place against the body. Asterisks (i.e. R1\* and R3\*) indicate electrodes inserted on the right side of the fish. The center of mass is represented by a gray circle.

between the skin and the vertebral column (Fig. 1; W2, W3). In addition, two red muscle electrodes were placed in corresponding longitudinal positions on the right side of the fish (denoted with an asterisk, R1\* and R3\*). At the end of the surgery, all eight implanted electrode wires were gathered, glued into one cable with cyanoacrylate (Fig. 1A) and anchored to a suture loop (4-0 gauge braided silk thread; Ethicon Inc., Somerville, NJ, USA) located on the back of the trout to prevent electrodes from being pulled out during the experiment.

After surgery (30–45 min), fish were transferred into a container of freshwater until a righting response was observed. They were then placed into a 600-liter recirculating flow tank ( $15 \pm 1^\circ\text{C}$ , working section  $28 \text{ cm} \times 28 \text{ cm} \times 80 \text{ cm}$ ) and allowed to recover for several hours before the start of an experiment.

#### Experimental procedures

To generate a Kármán vortex street, a 5 cm-diameter, D-section cylinder was used as in a previous study (Liao et al., 2003a). A RedLake high-speed digital video camera aimed at a  $45^\circ$  front-surface mirror placed below the flow tank recorded the ventral view of the trout ( $250 \text{ frames s}^{-1}$ ;  $1/500 \text{ s}$  shutter speed) against a lighted background.

Electromyography (EMG) and video data were simultaneously recorded for trout exposed to four treatment conditions: (1) holding station behind the cylinder placed in a flow of  $3.5 \text{ L s}^{-1}$ ; (2) in the absence of the cylinder, swimming in uniform flow at  $3.5 \text{ L s}^{-1}$ ; (3) in the absence of the cylinder, swimming in a slow, uniform flow ( $1.8 \text{ L s}^{-1}$ ) that approximated what would be the average, reduced flow velocity behind the cylinder (see Liao et al., 2003a) and (4) swimming in a fast, uniform flow ( $5 \text{ L s}^{-1}$ ) to elicit white muscle activity (to verify the viability of white muscle electrodes). EMG data were synchronized to video images with a voltage pulse trigger that simultaneously stopped video and EMG recording. Care was taken to analyze only those sequences in which fish were at least 3 cm away from the sides and bottom of the flow tank. EMG and kinematic data were collected from several fish for all treatment conditions. Data were analyzed from at least four tail-beat cycles for all five fish for treatments 1 and 2.

The following kinematic variables were measured; lateral amplitude of the head, the body at the R1 insertion site and the center of mass (COM) relative to the body midline, maximum head angle relative to the  $x$ -axis (Fig. 1B), body wavelength 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.

#### Data analysis

During data acquisition, EMG signals were amplified 10 000

times using Grass AC P511K preamplifiers with a 60 Hz notch filter and a 100 Hz high-pass and 3000 Hz low-pass filter, as in previous studies (Jayne and Lauder, 1993, 1995). A Powerlab 16SP analog-to-digital converter (ADInstruments, Colorado Springs, CO, USA) recorded digitized EMG signals at a sampling frequency of 4000 Hz. Signals were post-processed in Matlab (v.6.1) using a 10th order Butterworth filter (zero phase shifting) with a high- and low-pass frequency of 94 Hz and 1040 Hz, respectively. EMG variables such as intensity, duration, onset, offset and area were analyzed for each tail-beat with customized software. The relative intensity of each muscle burst was calculated as the mean spike amplitude for the rectified EMG signal normalized by the maximum mean spike amplitude observed. Duration was recorded as a proportion of the time elapsed relative to one cycle of the COM. Onset and offset times were measured relative to the start of the corresponding kinematic cycle of the COM. Rectified area, the product of relative intensity and duration, was measured and included in the calculation of means only if there were visible signs of muscle activity.

#### Statistical tests

Multiple linear regression analyses using a general linear model were performed and compared for both flow treatments to examine the idea that muscle activity would explain body kinematics during steady swimming but not during the Kármán gait because of the large effect of the vortices. The general linear model tested the simultaneous effect of independent EMG variables (muscle intensity, duration and relative onset time as well as their interactions) on each of the dependent swimming kinematics variables (head angle, head amplitude, R1 amplitude and center of mass amplitude). Note that statistical comparisons were conducted only for R1 muscle activity since R1 was the only electrode active during both swimming in uniform flow and the Kármán gait. Furthermore, R1 was not always active during the Kármán gait, occurring 62% of the time, while in the remaining 38% of the time no axial muscle activity was present. Thus, only 62% of all Kármán gait trials were statistically compared with R1 activity during swimming in uniform flow.

Inclusion of correlated variables in a general linear model, known as multicollinearity (Berry and Feldman, 1985), exaggerates  $r^2$  values and projects a tighter fit to the distribution of data describing the relationship between muscle activity and body kinematics. Two steps were taken as a conservative approach to account for multicollinearity. First, both EMG and kinematic variables were evaluated for independence using separate simple linear regressions before being included in the general linear model. For example, muscle intensity and duration were both included in the general linear model only because, when regressed against each other, their  $r^2$  value was lower than 0.50. Second, the general linear model was iteratively stepped through using the technique of 'backward elimination' (p. 431, Zar, 1999) to remove the EMG variables that had insignificant effects on the kinematic variables while still preserving the original  $r^2$  value.

To provide a consistent comparison with data from fish adopting the Kármán gait, the same multiple linear regression model was applied to data from fish swimming in uniform flow. Analysis of variance (ANOVA) was used to determine if the multivariable model relating muscle activity and body kinematics was significant at  $P < 0.05$  (Table 1). Means and standard errors were calculated for the rectified area, intensity

and duration of muscle activity for all individuals, with values normalized within an individual prior to pooling the data. Multiple tail-beat cycles from each individual across individuals were also pooled to calculate the mean tail-beat frequency, wavelength, head amplitude and head angle along with the corresponding errors. Unpaired  $t$ -tests were performed to determine which variable means were significantly different between live, Kármán gaiting trout and dead, towed trout. Bonferroni *post-hoc* corrections were performed at  $\alpha = 0.05$  whenever multiple tests were used (e.g. ANOVAs and  $t$ -tests; Rice, 1989). All statistical tests were performed in Systat version 9 (PC).

Table 1. Multiple linear regression analyses for electromyogram variables on selected kinematic variables

|                     | $r^2$ | d.f. | $F$ | $P$   |
|---------------------|-------|------|-----|-------|
| <b>Kármán gait</b>  |       |      |     |       |
| Head angle          | 0.62  | 5    | 2.6 | 0.11  |
| Head amplitude      | 0.22  | 4    | 0.7 | 0.65  |
| COM amplitude       | 0.22  | 5    | 0.4 | 0.81  |
| <b>Uniform flow</b> |       |      |     |       |
| Head angle          | 0.44  | 5    | 6.0 | 0.11  |
| Head amplitude      | 0.68  | 5    | 6.0 | 0.02* |
| COM amplitude       | 0.22  | 4    | 1.1 | 0.41  |

\*Significant after sequential Bonferroni correction at  $\alpha = 0.05$  ( $N = 5$  fish).  
COM, center of mass.

**Results**

*Patterns of muscle activity in uniform vs perturbed flow environments*

Trout swimming in uniform flow displayed a typical pattern of sequential, antero-posterior axial muscle activation. The proportion of the body encompassed by this wave of muscle activity depended on the swimming speed (Fig. 2). At the slowest swimming speed of  $1.8 L s^{-1}$  (Fig. 2A), the body wave was localized posteriorly; thus, only the two most caudal red

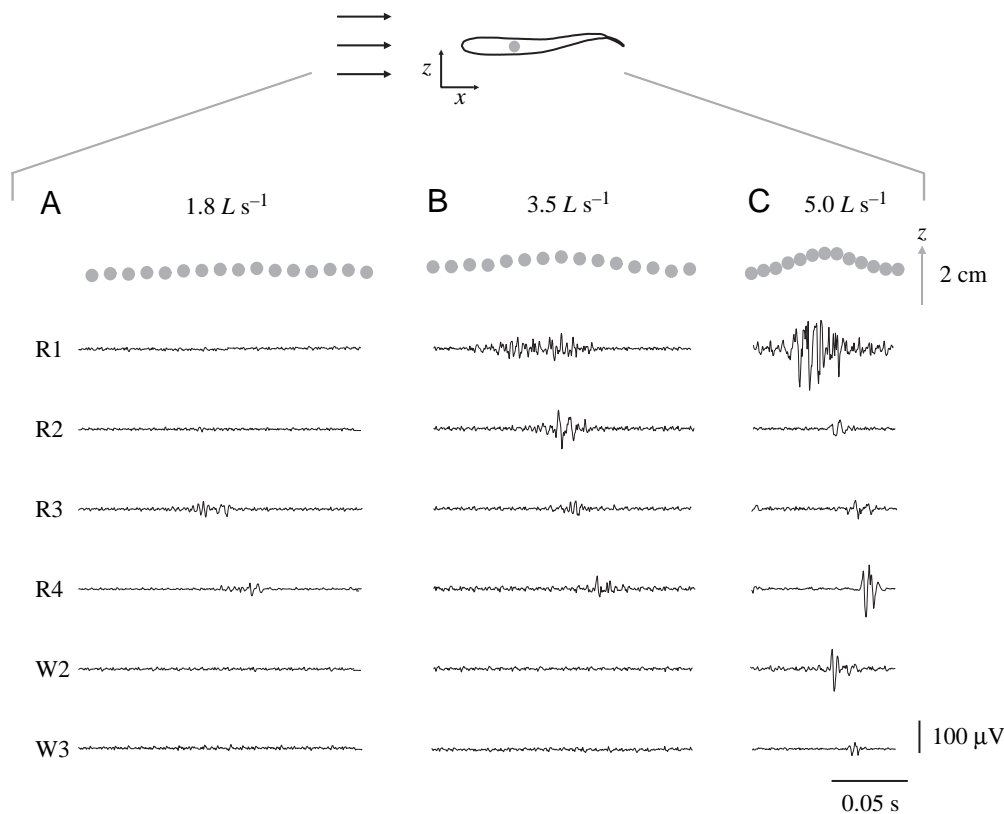


Fig. 2. Representative electromyograms from a trout swimming steadily in uniform flow at three speeds, along with the corresponding lateral ( $z$ -axis) excursions of the center of mass (COM; gray circles). At a flow speed approximating the reduced velocity behind the cylinder (A), only the posterior red muscles are active. At a flow speed of  $3.5 L s^{-1}$  (B), there is a propagating wave of red muscle activity down the entire body with no white muscle activity. When trout swam at the highest speed (C), anaerobic white muscles were recruited. At each swimming speed, staggered onset times of muscle activity down the body reflect the presence of a propulsive body wave. Scale bars for time (black, horizontal), electromyography intensity (black, vertical) and COM amplitude (gray) are shown.

muscle electrodes showed activity (R3 and R4). At a uniform flow speed of  $3.5 L s^{-1}$  (Fig. 2B), the anterior red muscles were additionally recruited so that the entire body participated in the propulsive wave. At the highest flow speed of  $5.0 L s^{-1}$  (Fig. 2C), anaerobic white muscles became active. By contrast, Kármán gaiting trout exhibited a fundamentally different, and

substantially reduced, pattern of rhythmic muscle activity (Fig. 3B,C). Although there was some spatial and temporal variability in red muscle activity, two strong patterns emerged, both of which represent a substantial departure from swimming in uniform flow at  $3.5 L s^{-1}$ . At times, only the anterior-most red muscles were rhythmically active on one side of the body (Fig. 3C; R1), while at other times, when paired fins were active, there was no appreciable axial muscle activity along the entire body (Fig. 4).

The average rectified area for each of the electromyograms from electrodes R2–R4, when averaged across several tail-beat cycles for each of five fish, was significantly lower during the Kármán gait than during swimming in uniform flow (Fig. 5A;  $P < 0.001$ ,  $n = 36$ ). There was no white muscle activity for either flow treatment. By contrast, the average rectified area for R1 activity was not statistically different between the two flow conditions. When R1 activity was present during the Kármán gait (Fig. 5B,C), it was marked by a lower relative intensity ( $0.33 \pm 0.05$  vs  $0.74 \pm 0.06$ ;  $P < 0.001$ ,  $n = 30$ ) and longer absolute duration time ( $0.18 \pm 0.03$  s vs  $0.06 \pm 0.01$  s;  $P < 0.005$ ,  $n = 30$ ) than that seen for R1 activity during swimming in uniform flow. Average, rectified R1 EMG traces for all five fish showed that relative onset time of R1 muscle activity (Fig. 6A,B) occurred earlier during the Kármán gait than for swimming in uniform flow at  $3.5 L s^{-1}$  ( $0.15 \pm 0.02$  vs  $0.28 \pm 0.03$ ;  $P < 0.05$ ,  $n = 30$ ). Similarly, relative offset time of EMG bursts occurred earlier for Kármán gaiting trout ( $0.50 \pm 0.02$  vs  $0.65 \pm 0.02$ ;  $P < 0.005$ ,  $n = 30$ ). As expected, trout swimming in uniform flow displayed caudal red muscle activity (R4) with delayed relative onset ( $0.53 \pm 0.02$  vs  $0.27 \pm 0.02$ ;  $P < 0.001$ ,  $n = 42$ ) and offset ( $0.71 \pm 0.02$  vs  $0.65 \pm 0.02$ ;  $P < 0.05$ ,  $n = 42$ ) times compared with

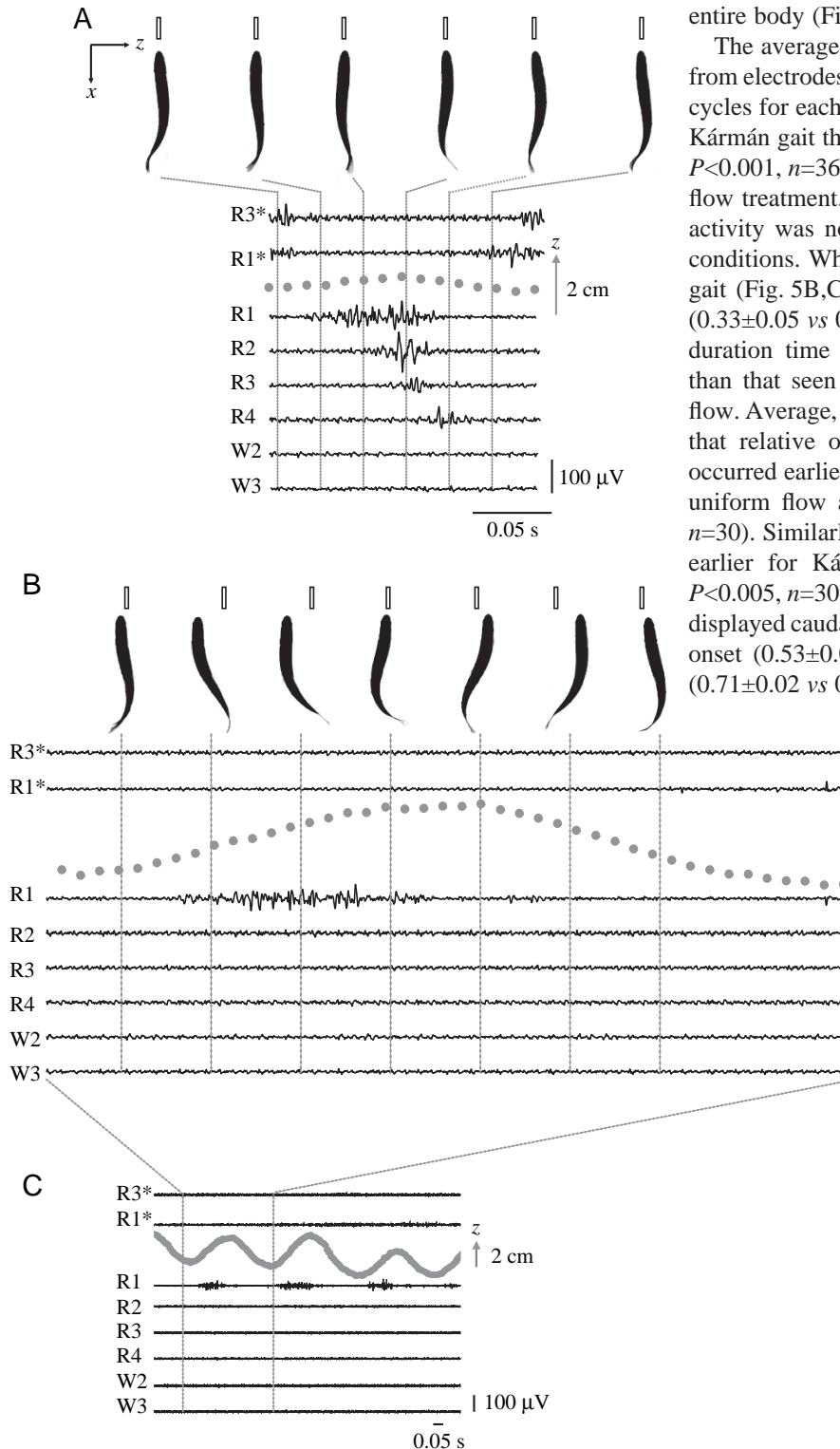


Fig. 3. Red and white axial muscle electromyography traces of a locomoting trout shown with corresponding ventral video images taken at evenly spaced intervals, for one oscillation of the center of mass. When swimming in uniform flow at  $3.5 L s^{-1}$  (A), waves of red muscle activity propagate down each side of the body. Open rectangles provide an arbitrary, fixed reference point to assess lateral body amplitudes. The same fish Kármán gaiting behind a cylinder placed in a  $3.5 L s^{-1}$  flow (B,C) activates its red muscles (R1) on one side of its body but not the other (R1\* or R3\*). B shares the same scale as A to facilitate comparison during one center of mass (COM) cycle. B is a subset of C, which shows the rhythmic nature of R1 activity. Open rectangles are aligned with the center of the cylinder, located approximately  $1.5 L$  upstream (not shown). Scale bars are given for time (black, horizontal), muscle intensity (black, vertical) and lateral amplitude of COM (gray).

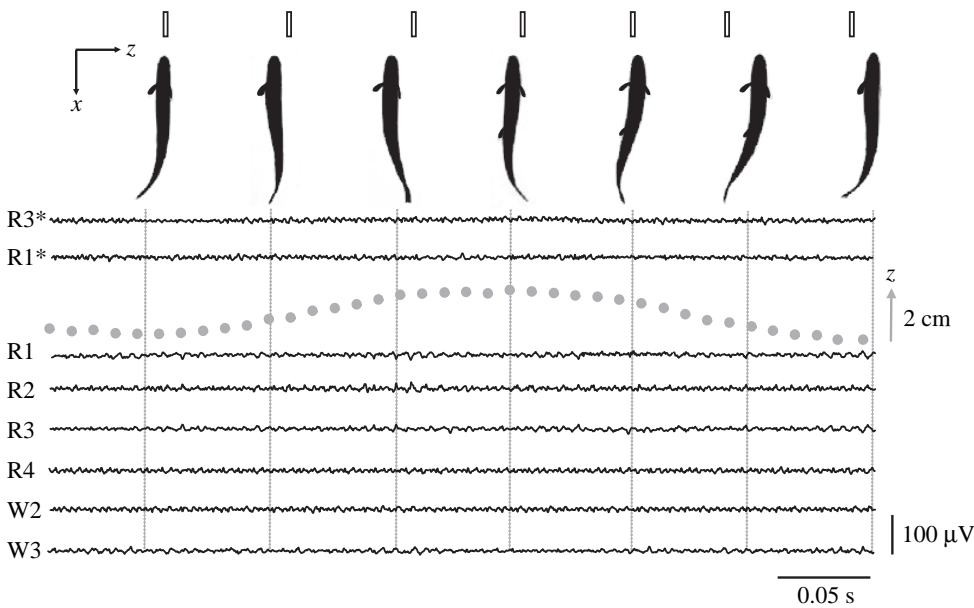


Fig. 4. At times when the paired fins are actively abducted during the Kármán gait, there is no appreciable axial muscle activity on either side of the body. Pectoral and pelvic fin silhouettes were digitized and enhanced to illustrate the pattern of abductions as the fish is buffeted from side to side by cylinder vortices. Open rectangles are aligned with the center of the cylinder, located approximately  $1.5 L$  upstream (not shown). Scale bars are given for time (black, horizontal), muscle intensity (black, vertical) and the lateral amplitude of the center of mass (gray).

anterior red muscle activity (R1), illustrating the presence of an antero-posterior propagating body wave (Fig. 6A,C). By contrast, this phase delay in muscle activity was not present for trout holding station in a vortex street because they did not activate their caudal red muscles (Fig. 6B,D).

#### Effect of muscle and vortices on kinematics

R1 muscle activity was correlated to certain kinematic variables during swimming in uniform flow but not during the Kármán gait. Specifically, R1 muscle activity was correlated to lateral head amplitude when trout swam in uniform flow (Table 1;  $r^2=0.68$ ,  $P<0.05$ ,  $n=20$ ) but not when trout Kármán gait ( $r^2=0.22$ ,  $P=0.65$ ,  $n=14$ ). According to the general linear model, head amplitude for trout swimming in uniform flow was significantly influenced by R1 muscle intensity, duration

and onset time (Fig. 7). R1 muscle activity was also correlated to head angle during swimming in uniform flow, but only before a sequential Bonferroni correction adjusted the  $\alpha$  level for the multiple independent tests required for the analysis. Note that a simple linear regression showed a correlation between head angle and head amplitude during swimming in uniform flow ( $r^2=0.30$ ,  $P<0.01$ ,  $n=36$ ). Head angle was not correlated to R1 muscle activity during the Kármán gait. Additional multiple linear regression analyses revealed that other kinematic variables during the Kármán gait, such as lateral body amplitude at both the R1 insertion site and the COM, were also not correlated to R1 muscle activity.

The motions of dead trout towed behind a cylinder were analyzed to gain insight into the contribution of passive, vortex-induced body undulation during the Kármán gait

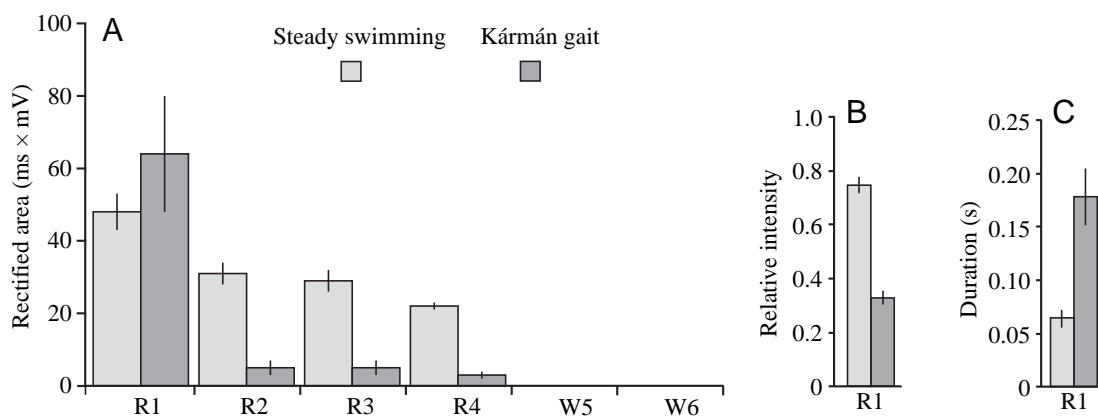


Fig. 5. (A) Average, rectified area of muscle activity (product of muscle intensity and burst duration) along the body for all five trout swimming in uniform flow at  $3.5 L s^{-1}$  (light gray bars) and Kármán gaiting in a vortex street (dark gray bars). Vertical lines indicate s.e.m. Note that there is no white muscle activity (W5 and W6) during either flow treatment. Compared with trout behind a cylinder, axial muscles of trout swimming in uniform flow have a significantly greater average rectified area for all locations down the body except R1 ( $n=20$ ). Kármán gait R1 muscle activity has a significantly lower intensity (B) but longer burst duration (C) than R1 muscle activity during swimming in uniform flow.

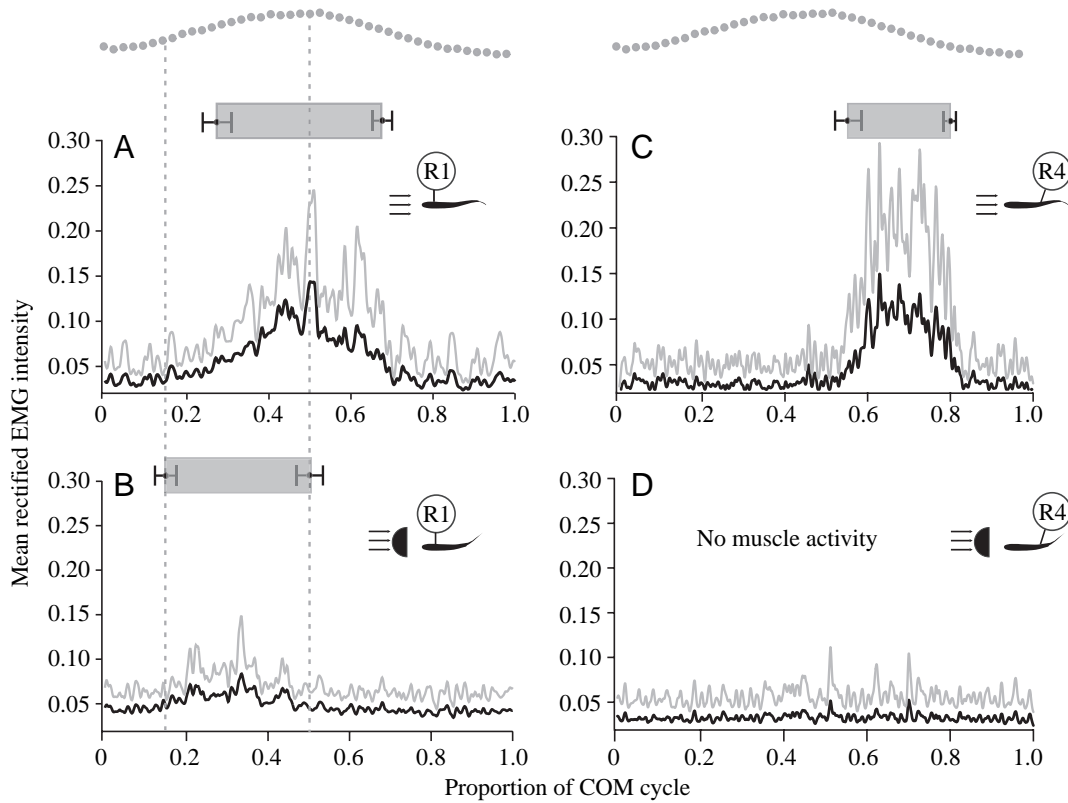


Fig. 6. Normalized, average rectified electromyograms of anterior (R1) and posterior (R4) red muscle activity (solid black line) along with the upper limit of the s.e.m. (solid gray line) for all five trout swimming in uniform flow (A and C;  $n=20$ ) and Kármán gaiting (B and D;  $n=14$ ). Data are shown relative to one oscillation cycle of the center of mass (COM; gray circles). Mean onset and offset times of muscle activity (horizontal gray bar) along with their s.e.m. are shown above each graph, where applicable. When trout are behind the cylinder (B), R1 onset and offset times (vertical broken lines) occur relatively earlier in the COM cycle than for trout swimming in uniform flow (A). (C) Rectified area for R4 during swimming in uniform flow ( $n=20$ ) shows delayed onset and offset times relative to A, indicating the presence of a propagating body wave. (D) By contrast, no posterior red muscle activity is present when trout Kármán gait.

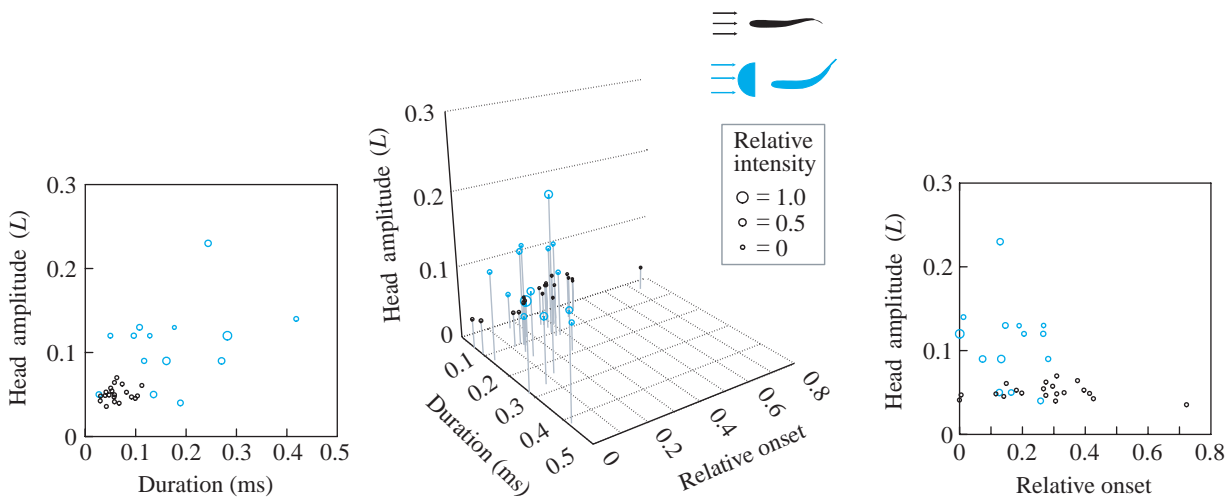


Fig. 7. Multiple linear regression model showing the relationship between lateral head amplitude and R1 muscle activity variables for trout swimming in uniform flow (black circles) and Kármán gaiting (blue circles). Circle diameters are scaled to illustrate the relative magnitude of muscle intensity. During swimming in uniform flow, head amplitude has a significant slope when plotted against burst duration and relative onset time ( $r^2=0.68$ ,  $P<0.05$ ,  $n=20$ ). Actual three-dimensional relationships of the data are plotted, along with corresponding two-dimensional deconstructions, on either side to facilitate interpretation. By contrast, during the Kármán gait, head amplitude is not correlated to muscle activity ( $r^2=0.22$ ,  $P=0.65$ ,  $n=14$ ).

Table 2. *Kármán gait kinematics and cylinder wake variables*

|                              | Dead trout | Live trout | Cylinder          |
|------------------------------|------------|------------|-------------------|
| Tail-beat frequency (Hz)     | 2.77±0.03  | 2.21±0.06  | 2.87 <sup>†</sup> |
| Body wavelength ( <i>L</i> ) | 1.47±0.07  | 2.14±0.08  | 1.22 <sup>†</sup> |
| Head amplitude ( <i>L</i> )  | 0.07±0.01  | 0.10±0.01  |                   |
| Head angle (deg.)*           | 16.15±0.01 | 15.05±0.10 |                   |

Values are means ± S.E.M.

\*Not significantly different between dead and live trout ( $P < 0.05$ ;  $N = 5$  fish).

<sup>†</sup>Value represents the expected vortex shedding frequency or the expected wake wavelength.

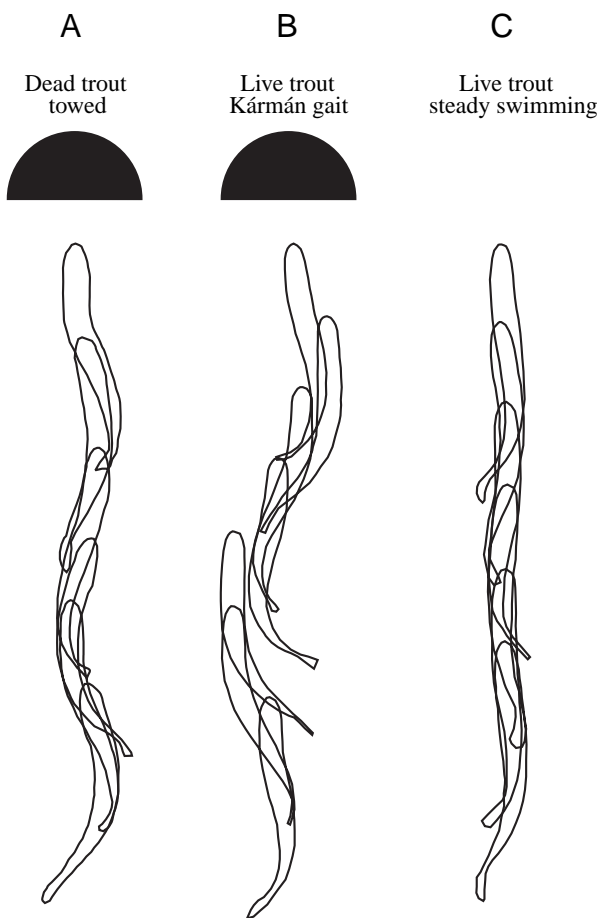


Fig. 8. Body outlines of a dead trout towed behind the cylinder (A), a live trout Kármán gaiting behind the cylinder (B) and a live trout swimming in uniform flow at  $3.5 L s^{-1}$  (C). Within each experimental treatment, body outlines have been displaced upstream at evenly spaced intervals to facilitate visualization of kinematics. Similar to a live trout Kármán gaiting, a dead trout towed in the wake of a cylinder oscillates laterally with high amplitude and has a tail-beat frequency similar to the expected vortex shedding frequency. The body wavelength is also longer than the expected wake wavelength, confirming that live fish can synchronize to the vortex street in a largely passive manner. Dead and live trout behind the cylinder adopt the same mean head angle. However, live trout head angles have a wider range of values and a higher variance, indicating a larger change in head angle during the Kármán gait compared with dead trout.

(Table 2). When dead trout were towed at  $3.5 L s^{-1}$  on low-stretch monofilament line in the region of the wake where live fish preferred to hold station ( $1.5 L$  downstream from the cylinder), their motions were generally similar to live, Kármán gaiting trout. However, quantitative kinematic analysis revealed that live trout have higher lateral head amplitudes than towed trout ( $0.10 \pm 0.01 L$  vs  $0.07 \pm 0.01 L$ , respectively;  $P < 0.05$ ,  $n = 26$ ). Live trout also exhibit lower tail-beat frequencies ( $2.21 \pm 0.06$  Hz vs  $2.77 \pm 0.03$  Hz;  $P < 0.001$ ,  $n = 26$ ) and longer body wavelengths ( $2.14 \pm 0.08 L$  vs  $1.47 \pm 0.07 L$ ;  $P < 0.001$ ,  $n = 26$ ). Only head angle was not significantly different between live and dead trout. Taking into account blocking effects introduced by placing the cylinder into the flow tank, the expected vortex shedding frequency for a 5 cm-diameter cylinder in a flow of  $3.5 L s^{-1}$  is 2.87 Hz, and the expected wake wavelength is  $1.22 L$  (see Liao et al., 2003a). Thus, the tail-beat frequency for dead trout is more closely synchronized to the expected vortex shedding frequency than for live trout. Similarly, the passive body of a dead trout adopts a wavelength that is closer to the wake wavelength than that adopted for live trout.

## Discussion

### *Axial muscle activity during the Kármán gait*

Although the entire body of a Kármán gaiting trout participates in a large-amplitude mechanical wave, only the anterior axial muscles need to be activated to consistently exploit vortices (Liao et al., 2003b). This novel motor pattern represents a fundamental deviation from previous work on freely behaving fishes, which documents either a sequential antero-posterior wave of axial muscle activity during undulatory locomotion in uniform flows (present study; Altringham and Ellerby, 1999; Gillis, 1998b; Hammond et al., 1998; Jayne and Lauder, 1994) or the simultaneous, unilateral activation of axial muscles during escape responses (e.g. Jayne and Lauder, 1993; Westneat et al., 1998). In addition, anterior muscle activity during the Kármán gait has a much lower intensity and longer duration than during steady swimming, characteristics that suggest a role more akin to modulating body posture and compliance rather than generating propulsive body movements. By quantitatively showing that trout decrease axial muscle activity when Kármán gaiting (Fig. 6), the present study offers a physiological mechanism to explain why fishes naturally associate with turbulent flows rather than uniform currents (Breder, 1965; Heggenes, 1988; Herskin and Steffensen, 1998; Hinch and Rand, 2000; Lacroix and McCurdy, 1996; Pitcher et al., 1976; Webb, 1998).

Field observations assume that fishes in current-swept environments hold station behind objects to save energy by drafting (Fausch, 1993; Heggenes, 1988; McMahon and Gordon, 1989; Shuler et al., 1994). However, when muscle recording and flow visualization techniques are employed, it is clear that trout holding station behind a cylinder are using the energy of the vortices and not just seeking refuge in reduced



flow (Liao et al., 2003b). The present study demonstrates that Kármán gaiting trout are not using a traveling wave of muscle activity to generate propulsive movements while swimming in the slower flow behind the cylinder, which would result in a muscle activity pattern similar to that shown in Fig. 2A. The anteriorly localized pattern of rhythmic muscle activity during the Kármán gait therefore reflects a shift in emphasis from propulsion to stability. When trout are unable to effectively utilize vortices in a vortex street, as when encountering extreme wake wavelengths or low vorticity in an environment with high levels of background turbulence, axial muscle activity is predicted to increase as propulsive movements are introduced into the Kármán gait.

#### *Contributions of muscle and vortices*

The paucity of EMG signals, despite whole body undulations, reveals that Kármán gait kinematics are largely dictated by vortices rather than generated by axial muscle activity. Put another way, an advancing region of low pressure down the body caused by passing vortices, rather than sequential muscle activation, causes the body to adopt a traveling waveform. When exposed to vortices in the cylinder wake, trout move with the transverse (Fig. 1;  $z$ -axis) component of the flow, generating enough thrust to balance drag to hold position relative to the cylinder (Liao et al., 2003a,b).

Anterior muscles are rhythmically active during the Kármán gait (R1, Fig. 3C; although see discussion below on passive thrust production). However, head amplitude is predominately determined by environmental vortices and not by muscle activity, since R1 muscle activity is correlated to head amplitude during swimming in uniform flow but not during the Kármán gait. This is not to say that muscle activity does not play a potentially important role in positioning the head favorably in the wake (e.g. muscle activity may help resist head movement caused by vortices), only that the muscles themselves are not controlling the absolute movement of the head at all times. The lack of correlation between Kármán gait kinematics and R1 muscle activity may be attributed to the fact that trout may also move their body with their paired fins (especially the pectorals), requiring further analysis of simultaneous paired fin and R1 muscle activity to explain body kinematics sufficiently. These results suggest that activation of anterior axial muscles and paired fins enables fine-scale adjustments to stabilize the body to hold station continuously in a vortex street. An ability to control body orientation with R1 muscle activity would lend support to the tacking hypothesis of station holding in a vortex street (Liao et al., 2003a), where the camber and angle of the body must alternate from side to side to consistently generate thrust forces.

#### *Paired fin function and the lack of axial muscle activity*

Paired fins vary widely in their movements during the Kármán gait, ranging from oscillating, bilateral motions to sustained, unilateral abductions. Analysis of simultaneous EMG and video data shows that when paired fins oscillate

during the Kármán gait, fish often do not exhibit any axial muscle activity (Fig. 4). As control surfaces located anterior to the COM, paired fins can play a large role in controlling forces generated from three-dimensional interactions between the body and vortices. For example, the increased drag produced by abduction of one pectoral fin was commonly observed to cause the body to yaw to the same side, thereby changing the head angle that might otherwise be changed by strong anterior muscle activity. Thus, trout pectoral fins function differently from that of classical labriform swimmers (Drucker and Jensen, 1997; Gibb et al., 1994; Walker and Westneat, 1997) in that they control body orientation rather than provide flapping propulsion. Like other fishes, trout use their pectoral fins for both self-correcting control (i.e. the fin is held out stationary from the body and not oscillated) and powered movements (i.e. when the fin actively moves relative to the body) to stabilize body position (Drucker and Lauder, 2003; Webb, 1998) and resist absolute upstream movement in a vortex street (Liao et al., 2003a). These observations suggest that paired fins may play a larger locomotory role in perturbed environments than in uniform flows. In addition, median structures such as the dorsal and anal fin can dramatically alter the lateral body profile and thus enhance the ability for vortex capture.

#### *Passive thrust production in an oscillating flow*

Both hydrodynamic theory and experimental data demonstrate that a passive (i.e. non-actuated) foil can generate thrust when placed in an oscillating flow (Beal, 2003; Bose and Lien, 1990; Wu and Chwang, 1975). As a foil heaves from side to side in an oscillating flow such as a Kármán street, its chord maintains a favorable angle of attack with respect to the incident flow and thus generates lift and thrust (Bose and Lien, 1990; Wu and Chwang, 1975). Thrust establishes a moment that acts to pitch the foil such that its trajectory across the oscillating flow proceeds at a beneficial lift-generating angle (Wu and Chwang, 1975). At predictable times during the foil's phase-locked oscillation cycle, the transverse flow velocity also generates lift forces that act in the direction of heaving, additionally facilitating the side to side motion of the foil. This phenomenon is impossible in uniform flow, which by definition is limited to a horizontal flow component (Fig. 1;  $x$ -axis). Since a flexible foil is a closer approximation to the undulating body of a fish than a rigid foil, Wu and Chwang's (1975) mechanism of passive thrust generation can be conceptually applied to a Kármán gaiting trout by treating the body as a series of linked, rigid foils where each foil is anchored to its neighboring foils. Differential flow velocity across both surfaces of a flexible foil can generate thrust much like a rigid foil. The flexible foil differs in that it can be dynamically cambered according to local flow conditions, such that the orientation of individual sections is angled to the incident flow in a time-dependent, and presumably favorable, manner. In theory, it is possible that a trout in which no axial muscles are activated can passively generate thrust while in a vortex street. This is supported by experimental data showing

that live trout can Kármán gait temporarily without any axial muscle activity (Fig. 4).

To test the hypothesis that trout can passively produce thrust when phase-locked in a vortex street, freshly killed trout were towed 1.5 *L* downstream from the cylinder. Experiments on euthanized animals have previously yielded valuable insight on the functional role of the musculoskeletal system's intrinsic properties during aquatic locomotion. For example, when dead anuran larvae were externally actuated to swim, their swimming kinematics and pattern of vortex shedding were similar to those of live larvae, supporting the finding that the posterior portion of the tail undulates passively in live animals (Wassersug and Hoff, 1985). Likewise, electrical stimulation of the precaudal muscles in dead pumpkinseed sunfish demonstrated that a mechanical body wave, once initiated, could propagate passively down the entire body (McHenry et al., 1995).

Dead trout towed downstream of the suction region of a cylinder (Liao et al., 2003a) not only synchronized their body kinematics to the vortex street but also frequently moved upstream on slack line, conclusively demonstrating that thrust can be generated passively. Note that towed rubber fish models of varying stiffnesses, and even frozen trout, once completely thawed, did not move upstream on slack line, indicating that proper body compliance is crucial for passive thrust generation in a vortex street. The oscillating body motions of dead, towed trout were generally similar to live, Kármán gaiting trout volitionally holding station behind the cylinder. In both cases, head angle was the same, posterior body oscillations were similar in amplitude, tail-beat frequency approached the vortex shedding frequency of the cylinder, and body wavelength was longer than the wake wavelength (Fig. 8A,B). Previous work has shown that Kármán streets with the same vortex shedding frequency but different wavelengths elicit similar head angles in trout (Liao et al., 2003a) but could not address whether head angle was a result of vortex buffeting or axial muscle activity. The present study shows that head angles are the result of vortex interactions and are not controlled by anterior red axial muscles. Statistically identical head angles in dead and live trout behind a cylinder (Table 2) support the idea that vortices may play a large role in automatically aligning the head angle to facilitate Kármán gaiting. This suggests that head angles in live fish need not be the result of anterior muscle activity or paired fin movements, given that fish are positioned an appropriate distance downstream from the cylinder. Therefore, as the result of the inherent compliance of their musculoskeletal system and their downstream positioning in a vortex street, trout can generate thrust in oscillating flows using a similar mechanism to that outlined for rigid hydrofoils (Wu and Chwang, 1975). These data reveal, paradoxically, that at times no axial muscle activity is needed for fish to hold station in turbulent flows.

Quantitative analyses show that Kármán gait kinematics do differ between dead and live trout. When dead trout synchronized to the vortex wake and moved forward on slack line, their body kinematics were analyzed for several tail-beats.

Compared with live trout, dead trout behind a cylinder have a relatively shorter body wavelength and higher tail-beat frequency, which not surprisingly is in closer accord to the hydrodynamic characteristics of the vortex street. Consequently, this suggests that Kármán gaiting live trout have a greater body stiffness than dead trout towed in the cylinder wake. However, live trout show no evidence of stiffening their body *via* simultaneous, bilateral muscle activation (Fig. 3C), as has been found previously for steadily swimming (Long, 1998) and startled (Westneat et al., 1998) fishes. Greater body stiffness in live trout, perhaps conferred by postural or tonic muscle activity (Brainerd and Monroy, 1998), may augment the ability to Kármán gait continuously in a vortex wake.

Towed trout frequently pitched and rolled about their body axis. As a result of this instability, dead trout spent proportionately less time Kármán gaiting than did live trout. That is, when towed trout stabilized enough to Kármán gait they were more frequently drawn upstream into the suction region than live trout, ultimately coming into physical contact with the cylinder. The paired fins of dead trout were not observed to be passively abducted by the unsteady flows of the vortex street. This seems to suggest that paired fins play a key role in stabilizing the body in the vortex street by generating drag rather than by producing thrust. Therefore, the ability to Kármán gait continuously relies on the selective ability to produce drag to stay in the appropriate downstream region of the vortex street and avoid the suction region rather than on active body undulation to produce thrust. The difference in kinematics between dead and live trout emphasizes that, while a fundamental component of the behavior may be passive, the ability to Kármán gait consistently requires active control.

#### *A novel pattern of rhythmic muscle activity in swimming fish*

The concept of a central pattern generator (CPG) may provide a valuable framework to understand the novel pattern of muscle activity during the Kármán gait. CPGs are coordinated networks of neurons that can produce rhythmic body movements such as swimming in the absence of sensory feedback (Brown, 1914; Cohen et al., 1988; Grillner and Wallén, 1985). Spinal preparations of lampreys and dogfish have taken advantage of this fact and contributed enormously to our understanding of the feedforward aspects of CPGs (Cohen and Wallén, 1980; Grillner, 1974; Grillner and Wallén, 1984). Despite wide recognition that sensory feedback is an integral part of CPGs during natural behaviors (Cohen, 1992; Grillner and Wallén, 1984), data on how environmental conditions can alter CPGs during adaptive locomotion are less forthcoming (but see Sillar and Roberts, 1992). Along these lines, turbulent flows characteristic of many aquatic environments pose a unique challenge to the neuromuscular system of fishes because they warrant an adaptive response; a fish must be able to accommodate potentially destabilizing flows while still generating motor commands to provide propulsion.

The ability to Kármán gait continuously (*vs* short bouts in dead, towed trout) requires sensory feedback. When trout

respond to periodic vortices, such as are commonly shed behind inanimate objects in flow and by propulsive animals (Webb, 1998; Weihs, 1973), they display a motor pattern unlike that of any documented for swimming fish. Kármán gaiting trout abandon the sequential muscle contraction template of steady undulation and reveal the ability to decouple segmental muscle activity both down and across the body. Does the ability to selectively shut off motor output in all but the anterior-most region of an undulating body provide evidence for the modulation of a pre-existing CPG? Studies have demonstrated that multiple CPGs exist along the spinal cord and can generate rhythmic activity independently of their neighbors (Grillner and Kashin, 1976; Grillner and Wallén, 1984). While the periodic nature of a vortex street offers a tractable system by which to study how animals interact with vortices, at the same time exposing a moving animal to a rhythmic stimulus poses a challenge in interpreting the animal's motor response. Is the rhythmic muscle activity of the Kármán gait due to the action of a CPG or is it simply a local feedback response to periodically encountered vortices?

A study based on kinematics and EMGs alone cannot conclusively answer this question; both mechanisms are feasible. However, the following two lines of evidence would certainly suggest that Kármán gait muscle activity could be under the influence of a CPG. First, if indeed under the control of a CPG, Kármán gait muscle activity should exist in the absence of sensory feedback. This hypothesis could be tested by blocking the sensory systems of trout to see if they could still Kármán gait continuously. The ability to do so would suggest that a default motor program exists and it has been entrained to an external stimulus. Evidence for CPG synchronization to an external stimulus already exists in fishes; the rhythmic, undulatory movements of spinal dogfish and lampreys can readily be made to entrain on a physical or hydrodynamic stimulus (Grillner, 1974; Grillner and Wallén, 1984). In the absence of two major sensory modalities, vision and the lateral line (responsible for detecting water flow), trout have been shown to continuously hold station behind a cylinder (Montgomery et al., 2003; J. C. Liao, manuscript in preparation). These data suggest that trout may be employing a default motor pattern and are not just reacting reflexively to the presence of local vortices. Second, if a vortex was additionally introduced out of phase to the shedding cycle of the cylinder and elicited a motor response, this would imply that fish are reacting to vortices on a case by case basis. However, if the introduced vortex does not elicit a motor response but instead the motor output pattern continues to track the default frequency imposed by the cylinder shedding frequency, this would suggest that there is indeed a pattern generator at work. Alternatively, shed vortices could be abruptly stopped to see if fish still exhibited rhythmic motor patterns of the same frequency as the vortex shedding frequency. This could be accomplished by generating vortices with a vertical strut (as in Webb, 2004) oriented along the plane normal to the flow instead of a cylinder, with a sudden rotation of the strut parallel to the flow causing a stop in vortex generation.

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