Sensory integration in the hydrodynamic world of rainbow trout

J. C. Montgomery^{1*}, F. McDonald¹, C. F. Baker¹, A. G. Carton¹ and N. Ling²

¹Leigh Marine Laboratory and School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand

²School of Biological Sciences, University of Waikato, Hamilton, New Zealand

* Author for correspondence (j.montgomery@auckland.ac.nz).

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Water movements, of both abiotic and biotic origin, provide a wealth of information for fishes. They detect these water movements by arrays of hydrodynamic sensors located on the surface of the body as superficial neuromasts and embedded in subdermal lateral line canals. Recently, the anatomical dichotomy between superficial and canal neuromasts has been matched by demonstrations of a corresponding functional dichotomy. Superficial neuromasts are sensitive to water flows over the surface of the fish and are the sub-modality that participates in orientation to water currents, a behaviour known as rheotaxis. The canal neuromasts are sensitive to water vibration and it is this sub-modality that determines the localization of artificial prey. Recently, however, it has been shown that the complex behaviour of natural prey capture in the dark requires input from both lateral line sensory sub-modalities and here we show that the ability of trout to hold station behind a stationary object in fast flowing water also requires integration of information from both sub-modalities.

Keywords: hydrodynamic; lateral line; trout

1. INTRODUCTION

The lateral line system of fishes has long been divided anatomically into superficial and canal neuromast systems (figure 1). Superficial neuromasts are patches of mechanosensory hair cells on the surface of the skin of fishes. A gelatinous cupula overlies the hair cells and provides a mechanical coupling of the flow over the surface of the skin to the deflection of the cilia of hair cells. Canal neuromasts are larger, contain many more hair cells and are located within subdermal canals (Montgomery *et al.* 2002). Recently, considerable progress has been made in understanding the functional implications of this anatomical dichotomy and the role of these lateral line sub-modalities in fish behaviour.

Superficial neuromasts are sensitive to water flows over the surface of the body (Voigt *et al.* 2000). In still water, they also encode the oscillating flows generated by a vibrating source, but lose this ability in the presence of a background flow (Engelmann *et al.* 2000). Narrow lateral line canals operate as high-pass mechanical filters and shelter canal neuromasts from direct flows (Denton &

Gray 1983) such that they respond to oscillating sources both in still water and in the presence of a background flow (Engelmann *et al.* 2000). This front-end mechanical filter is presumed to permit an increase in sensitivity of canal neuromasts generated by their larger size and greater number of hair cells. In line with the above functional division of labour, it has been shown that the superficial neuromast system, but not the canal system, participates in rheotaxis, or the orientation of fishes to water currents (Montgomery *et al.* 1997). Ablation of the superficial system in three diverse species of fish significantly elevated the threshold current velocities at which the fish faced upstream, whereas, pharmacological blockade of the canal system had no effect (Montgomery *et al.* 1997). By contrast, the canal system has been shown to be responsible for the orientation behaviour of mottled sculpin to artificial prey (Coombs *et al.* 2001). Mottled sculpin approach and attack a small vibrating bead, a behaviour that is disrupted by a pharmacological block of the canal system, but unaffected by ablation of the superficial neuromasts.

Rheotaxis and orientation to an oscillating source are behaviours where the individual role of these sensory modalities is clear-cut. Other behaviours, however, may require the central integration of input from both modalities. Subsequent to the demonstration of hydrodynamic-trail following by fishes (Pohlmann *et al.* 2001), it was shown that both superficial and canal modalities were required for rainbow trout to successfully capture piscine prey in the dark (Montgomery *et al.* 2002). The requirement for both sensory modalities to be used in hydrodynamic-trail following most probably reflects the need for the predator to use both the flow and the turbulence information contained in the wake to successfully track the prey (Hanke *et al.* 2000). Hydrodynamic trails are left not only behind animals swimming in still water, but also behind stationary objects in flowing water. Do the same considerations as above apply for fishes holding station behind such objects?

Rainbow trout are highly efficient stream dwellers. Their ability to use the effects of bottom topography on water currents to their advantage is well known. They can hold station with a minimum of effort by positioning themselves with respect to objects, such as rocks, that disrupt the flow. This ability is known as object entrainment, and is mediated by both visual and hydrodynamic information (Sutterlin & Waddy 1975). Does the hydrodynamic information important to this behaviour contain both flow and turbulence components, and do trout need to integrate information from both lateral line sub-modalities to entrain successfully?

2. MATERIAL AND METHODS

The object entrainment experiments were conducted in a rectangular flume (8 m long and 500 mm wide with a water depth of 180 mm; figure 2). The mid-section of the flume was divided into three lanes (620 mm long and 167 mm wide) with flow baffles at the upstream and downstream end of each lane, and a 20 mm diameter plastic pipe standing in the centre of the lane. Individual trout (*Oncorhynchus mykiss*, 94–120 mm in total length) were introduced to each lane, and given 1 h at a flow rate of 31 cm s⁻¹ to adjust to their new environment. Flow rate was then increased to 42 cm s⁻¹ to induce entrainment behaviour and the fishes were filmed for 15 min under dim infrared light. Subsequently, the location of the fishes was recorded at 20 s intervals over the 15 min experimental period. For data analysis, each lane was divided into six equal zones, with entrainment defined as being located within the zone adjacent to, and downstream of, the obstacle. The primary data consisted of the proportion of time spent within this zone in comparison with the time spent in the other five areas. This proportion was found for 11

Figure 1. Illustration of the distribution of superficial neuromasts (small filled circles, arrowed) and canal pores (large filled circles) on *Oncorhynchus mykiss*. The number of superficial neuromasts differed slightly (one to three neuromasts) between the three fishes used for the SEM procedure.

Figure 2. (a) A trout (T) positioning itself off the wake of the obstacle (O) during obstacle entrainment. (b) Grid map of the experimental section of the flume showing the representative position of a trout (T) in relation to the obstacle (O) during control and sham operation trials. Each dot represents the position of the trout every 20 s. The large arrow represents the direction of the flow.

fishes in each of five groups, controls, sham-operated controls and three treatment groups. Treatments consisted of a pharmacological blockade of the entire lateral line with streptomycin sulphate (11 mg l^{-1} ; Kaus 1987), blockade of only the canal neuromasts with gentamicin (0.002%; Song *et al.* 1995), and physical ablation of the superficial neuromasts using a probe cooled in liquid nitrogen. The sham-operated control used the same probe applied to a comparable area of the head of the trout away from the location of the neuromasts. The location of the superficial neuromasts (which had not previously been reported in trout) was determined using conventional scanning electron microscopy on three fishes.

Figure 3. Average proportion of time spent entraining by the five different groups (error bars represent 95% confidence interval). Control and sham-operated controls were not significantly different from each other, but were different from each of the three treatment groups. The three treatment groups were not different from each other, or from what would be the expected fraction of time spent in that section of the tank if the fish movements were random.

3. RESULTS

The distribution of the superficial neuromasts and canal pores on the head and the body of the rainbow trout are shown in figure 1. Both subsystems fit the general pattern described on the head of many teleost fishes. However, rainbow trout possess a low number of superficial neuromasts, with only five neuromast lines over the cephalic region. These lines are found surrounding the olfactory nares, and on the supratemporal and pre-opercular regions.

At the flow rates used, intact or sham-operated trout entrained behind the obstacle 70% of the trial period, typically behind and to one side of the obstacle (figure 2). Individual fishes tended to have a handedness, meaning that they would entrain on one side of the object for the majority of the trial. There was no significant difference between intact and sham-operated fishes (one-way ANOVA followed by a *post hoc* Tukey's HSD multiple comparison test; figure 3). Both these groups entrained for a significantly higher amount of time compared with the treatment groups. Treatment with streptomycin (entire lateral line block) or gentamicin (canal block), or ablation of superficial neuromasts dropped entrainment to *ca.* 25%. Treatment groups were not significantly different from each other or from the proportion of time expected to be spent at random in that particular zone.

4. DISCUSSION

Previous work showed that cutting the posterior lateral line prevented trout from successfully entraining behind an object in the dark (Sutterlin & Waddy 1975). This demonstrates the importance of the canal subsystem for object entrainment, but leaves open the question as to whether the superficial neuromast system was also important in this behaviour. Our results clearly demonstrate the requirement of both lateral line sub-modalities for this task. During control trials with intact or sham-operated fishes, object entrainment occurred 70% of the time. Removal of sensory input from either lateral line sub-modality effectively prevented successful entrainment.

The requirement for both sensory modalities to be used in object entrainment most probably reflects the need for the trout to use both the flow and the turbulence information contained in the wake behind stationary objects to successfully hold station. Holding station behind an obstacle in the flow can be considered a special case of using local flow conditions during upstream movements to minimize energy expenditure and also the potential recovery of energy from vortices (Liao *et al.* 2003). It is possible that these behaviours will also have similar sensory requirements.

Behaviours, such as rheotaxis (Montgomery *et al.* 1997) and localization of oscillating objects (Coombs *et al.* 2001), have been important in identifying the division of labour between superficial and canal neuromasts. It may have been tempting to interpret this division of labour as a split between flow detection and prey detection. However, the more complex task of live prey capture, where the predator must track a moving prey item, requires the integration of information from both lateral line sub-modalities. Obstacle entrainment, which is more akin to flow detection, also requires integration of information from both lateral line sub-modalities. The hydrodynamic world of aquatic organisms is complex and a potentially rich source of information. It is not surprising that separate sensory channels have evolved to partition the information available into discrete subsets. It is also perhaps not surprising that this information is integrated by the

central nervous system for the execution of complex hydrodynamically mediated behaviours.

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