

Web Topic 7.1

Cilia and Sensory Receptors

Introduction

Cilia and flagella are widely used by eukaryotic organisms for locomotion, stimulus reception, or both. Although separate names were originally assigned to these organelles depending upon their size and the number per cell, the internal structure and functions of cilia and flagella have turned out to be identical. We shall thus refer to all such organelles as cilia. One of the most intriguing questions is *why* cilia have been recruited so often as sensory receptors. Below, we provide a general review of how ciliary structure appears to be correlated with function, and outline some possible reasons for their use as receptor devices.

Cell skeletons and cilia

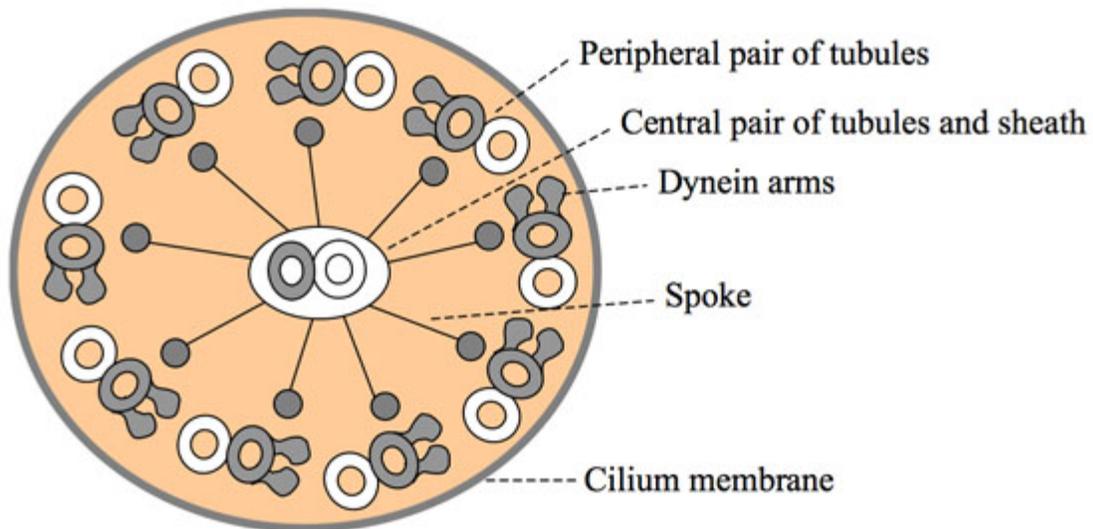
Animal cells require an internal scaffolding or **cytoskeleton** to hold their shape. A mesh of actin protein filaments usually underlies most cell membranes. This cell surface support is complemented by a network of intermediately sized proteins that maintains the three-dimensional structure of the cell's cytoplasm. Finally, the **centrosome** of the cell, consisting of two perpendicularly oriented **centrioles**, produces a third meshwork of **microtubules** throughout the cell that is used for additional support and as "rails" for the transport of internal cell components. The centrosome network also mediates the partitioning of cellular components during cell division. These microtubules are largely composed of **tubulin** proteins. Each centriole is a barrel-shaped organelle whose walls consist of parallel microtubules arrayed into nine clusters with three tubules per cluster.

Animal sensory cells respond to stimuli by varying the permeability of specific ion channels in their membranes. This changes the ionic composition inside the cell's cytoplasm, produces a change in electrical fields across the cell membrane, or both. Either effect is maximized when the area of the responding cell membrane is large relative to the volume of cytoplasm that it encloses. There are several ways sensory cells can achieve this high surface area/volume ratio. One is to elaborate the membrane surface exposed to stimuli into a large number of small fingers called **microvilli**. The membrane surrounding each microvillus is continuous with the overall cell membrane, and actin filaments that extend from the mesh under the cell membrane into the cytoplasm of the microvilli provide the necessary support (Cooper and Hausman 2007). An alternative is to place one or more **cilia** on the exposed cell surface. Like microvilli, the membranes enclosing each cilium are continuous with the adjacent cell membrane. The cytoplasm inside the cilium is usually somewhat isolated from that in the rest of the cell by a **terminal plate** at its base (Singla and Reiter 2006). Cilia differ from microvilli in that they are typically larger in both diameter and length, and their support is provided by parallel microtubules generated by adjacent centrioles. Whereas the centrioles consist of nine **triplets** of parallel microtubules, the cilia attached to them usually have nine or more **pairs** of microtubules forming an internal cylinder of support. The ensemble of parallel pairs of tubules in a cilium is called its **axoneme**.

Structural types of cilia

Cilia can usually be assigned to one of two classes depending upon their axoneme structure:

- **9+2 Cilia**: The axoneme of most motile cilia and flagella contains nine pairs of parallel tubules arranged around the periphery of the ciliary interior. These tubules are continuous with those in one of the centrioles (called the **basal body**) just beneath the base of the cilium. A tenth pair of tubules runs along the center of the cilium and is usually surrounded by a thin sheath. This configuration is thus called a **9+2** (or $9 \times 2 + 1$ pair) design. Each of the peripheral pairs of tubules extends inner and outer **arms** made of the protein **dynein** towards the next pair of tubules. There is usually a spoke connecting each peripheral pair of tubules to the sheath surrounding the central tubules. A cross section of a 9+2 cilium near its base thus looks like this:



Closer to the tip of the cilium, the pairs of peripheral tubules may merge into a single tubule and the central pair may disappear. Although discovered first, these are often called **secondary cilia**.

- **9+0 Cilia:** Members of this class of cilia lack the central tubules, spokes, and dynein arms described above. It is thus described as a 9+0 configuration. Some species have a 9+0 configuration at the base of the cilium, but this gradually turns into 8 pairs of tubules in the periphery and one central tubule (e.g., 8+1) (Zakon 1986; Whitfield 2004). At the very tip, 9+0 cilia often contain only a few remaining tubules and their relative disposition is highly variable. 9+0 cilia often have conspicuous links between the two underlying centrioles with the more internal one generating a large root into the cytoplasm (Yack 2004). Cilia with the 9+0 structure are often called **primary cilia** because they appear so widely in vertebrates and many other animal taxa. Nearly all vertebrate cells except ova, including nerve cells, host a single primary cilium with a 9+0 configuration and usually no dynein arms or spokes at some point in development (Whitfield 2004; Praetorius and Spring 2005; Singla and Reiter 2006; Christensen et al. 2007).

Ciliary function

As noted earlier, cilia can have either or both of two functions: (a) propelling the organism and/or the adjacent medium relative to each other by beating rhythmically, and (b) acting as sensory receptors. It was originally believed that 9+2 cilia were always motile and locomotory organelles, whereas 9+0 cilia were always immotile and sensory in function (Satir 1977). Subsequent studies have shown that a variety of combinations of structure and function exist in nature (Ibañez-Tallon et al. 2003). We give examples below of some of these combinations:

- **Locomotory (motile) cilia:** These cilia (and flagella) provide propulsion for small organisms, or create currents of adjacent medium for larger and/or sessile ones. Cilia are very widely distributed on the external surfaces of aquatic invertebrates. However, even terrestrial vertebrates may use internal cilia to keep airways clear of dust and particles, and to move gametes around in reproductive organs. Most motile cilia have a classic 9+2 structure, and their physiology is well understood. Their major task is to beat by bending first in one direction and then the other in a repetitive manner. Studies have shown that the dynein arms on the outer tubules of their axonemes are the biochemical motors that generate the bending (Karp 2007). They do this by grabbing the nearest adjacent tubules and “burn” ATP fuel to power a ratcheting movement along the length of the other tubule. Since they are rooted to a separate pair of tubules, their movement causes adjacent pairs of tubules to slide past each other. The central pair of tubules are asymmetric and appear to coordinate the temporal patterning of a beating stroke (Porter and Sale 2000). Their action is communicated through the spokes to the inner dynein arms of each pair of peripheral tubules that then define the amplitude and waveform of the stroke. The outer dynein arms respond by doubling the frequency of beating and adding power to each stroke.

Although the central tubules, spokes, and dynein arms were all thought to be essential for rhythmic beating, the embryos of many vertebrates have special 9+0 **nodal cilia** on their ventral surface that are essential for normal development. These cilia lack central tubules and spokes, but they do have special dynein proteins that allow them to beat in a rotational manner. This beating causes currents that are necessary to establish the left-right asymmetry of the developing embryo (Ibañez-Tallon et al. 2003; Praetorius and Spring 2005).

- **Sensory cilia:** Multiple examples of ciliary receptors exist for every sensory modality used in animal communication: vision, audition, olfaction, touch, hydrodynamic reception, and electroreception. The relevant axoneme structures vary with both modality and taxon:
 - *Mechanoreception, audition, and hydrodynamic detection:* The external hairs and trichobothria, scolopale ears, and substrate sensitive mechanoreceptors of arthropods typically contain a 9+0 ciliary segment (Keil 1997; Yack 2004). Those in some insects may be motile despite the lack of a central pair of tubules (Göpfert and Robert 2003). The detectors inside mammalian kidneys that monitor fluid flow also rely on 9+0 cilia for stimulation. In contrast, the kinocilia of vertebrate lateral lines, vestibular organs, and ears are all 9+2 ciliary structures (Popper and Fay 1999). No known vertebrate touch receptors rely on ciliary components for stimulation.
 - *Electroreception:* Only the ampullary electroreceptors of primitive fish have a ciliary component; the ampullary-like and tuberous receptors in teleosts have microvilli instead. Where examined, the cilia of primitive fish electroreceptors show a 9+0 configuration at the base that changes into an 8+1 design for most of its length (Teeter et al. 1980; Zakon 1986).
 - *Photoreception:* Photoreceptors in jellyfish (Cnidaria) include a ciliary structure with a 9+2 axoneme (Eakin 1982). More advanced animals may have either microvillar (rhabdomeric) or ciliary photoreceptors, and some species have one type in their eyes and the other type located in the brain or some other tissue for monitoring circadian cycles (Arendt 2001; Arendt and Wittbrodt 2001; Arendt et al. 2004). Where ciliary photoreceptors are present, most have a 9+0 structure (Eakin 1979, 1982), but there are exceptions such as the 9+2 receptors in the larval eyes of snails (Blumer 1994). Both rhabdomeric and ciliary photoreceptors begin development with a 9+2 cilium: rhabdomeric photoreceptors entirely lose the cilium as they mature, whereas the ciliary photoreceptors tend to retain at least the outer pairs of axoneme tubules (Yamada 1982; Arendt and Wittbrodt 2001).
 - *Olfaction:* Whereas some crustaceans have 9+2 cilia in their chemoreceptors, most insect chemoreceptors use 9+0 cilia (Grünert and Ache 1988). Vertebrate chemoreceptors favor 9+2 cilia, and many are known to be motile as well as sensory (Lidow and Menco 1984).
- **Primary cilia and development:** Primary cilia have turned out to have critical signaling functions during vertebrate development, and possibly in other metazoans (Goetz and Anderson 2010; Louvi and Grove 2011; Vincensini et al. 2011). As noted earlier, most vertebrate cells host a primary cilium, at least early in development, and these appear to be the main “sensory” organelles by which embryonic cells respond to the hedgehog signaling pathway. Development creates different concentrations of hedgehog proteins in different parts of the embryo, and these influence what type of tissue and organ each cell will become as well as differentiating the main body axes. Mutants with defective ciliary functions exhibit major deformities and disfunctions as a result. The intrinsic sensory properties of cilia (see below) make them ideal targets for this type of developmental regulation.

Cilia as preadaptations for sensory receptors

Several factors, either singly or in concert, appear to have pre-adapted cilia as sensory receptors:

- **Phylogenetic history:** As discussed in Chapter 7, cilia of single-celled eukaryotes are often responsive to touch and other stimuli. This requires the presence of suitable ion channels in their membranes that can be coupled to appropriate stimuli (Hegemann 1997; Machemer et al. 1998; Govorunova et al. 2004). In most cases, stimulation

triggers the admission of calcium ions and either chemical cascades and/or electrical field changes across the cell membrane. These mechanisms of single-celled eukaryotes were retained in early multicellular organisms, and thus provided a significant preadaptation for subsequent specialization of somatic sensory cells (Praetorius and Spring 2005).

- **Internal transport system:** All cilia, whether motile or immotile, have a system for transporting small particles and intracellular components inside the ciliary cytoplasm (Scholey 2003; Praetorius and Spring 2005; Inglis et al. 2006; Singla and Reiter 2006). This transport system uses the axoneme as a scaffolding: kinesin motors move components from the base to the tip of the cilium, and dynein motors move components in the opposite direction. Since most organisms resorb their cilia or flagella before cell division, ciliary reconstruction is a frequent event (Quarmany and Parker 2005). All materials for building and repairing cilia must come from the main body of the cell (usually the Golgi apparatus), and are passed through the selective pores of the terminal plate at the base of the cilium. They are then attached to a protein transport particle and moved along the axoneme to their site of usage. After discharging their cargo, the transport particles are carried back to the base of the cilium and readied for another cycle (Rosenbaum and Witman 2002). In addition to the building of a cilium, the transport system provides fuel for motile cilia and flagella, and transports signals stimulated by ciliary membrane receipt of developmental regulators (such as the hedgehog proteins), down to the host cell body where they modulate cell activities.

The ciliary transport system also plays a critical role in sensory receptors. Most sensory organs respond to outside stimuli continuously. Once stimulated, a sensory cell must restore itself to its prior sensitive state as soon as possible. This will invariably require rapid and massive transport processes: ions that entered the cell upon stimulation must be moved back out; photoreceptor pigments denatured by absorbing light must be restored at some energetic cost; chemical cascades begun when olfactory or light stimuli hit a cell must be retriggered for the next stimulus. The internal transport system originally evolved to provide fuel for beating cilia was an excellent preadaptation for restoring sensory receptors back to pre-stimulus conditions quickly. This is surely one reason why cilia have so often been recruited into sensory organs (Christensen et al. 2007).

- **Ubiquity:** Motile cilia occur on the external body surfaces of nearly all aquatic invertebrates (Brusca and Brusca 2003). Terrestrial arthropods usually do not have external cilia, but they use them widely inside their bodies. The sensory functions of primary cilia after development is complete are only beginning to be appreciated. At a minimum, primary cilia may act as mechanoreceptors to detect local flows of medium or movements of adjacent cells and thus coordinate activities of cells in a given region. There is also evidence that they may act as chemosensory aeries by absorbing extracellular chemical signals released by other cells and conveying them, using their internal transport system, to the cytoplasm of their own cell. These broad sensitivities have clearly been exploited by vertebrates to regulate differentiation during development. Whatever the function(s) that have generated it, the ubiquity of primary cilia in vertebrates and motile cilia in other taxa clearly enhances the chance that some will be recruited over evolutionary time into new locations and types of receptors.

Ciliary versus non-ciliary receptor systems

Given the abundant reasons why cilia might be recruited into sensory organs, why are they not the only such source? The fact is that they are not. While all vertebrates so far examined have primary cilium sensitivity to hedgehog proteins, this is not the only way that cells can respond to hedgehog proteins, and the latter are not the only way that cell differentiation during development is regulated (Goetz and Anderson 2010; Vincensini et al. 2011). *Drosophila* development proceeds with a type of hedgehog proteins, but cilia do not play an important role in signaling. We noted above that photoreceptors exist in both ciliary and rhabdomeric configurations, and that each has its own set of photoreceptor (opsin) proteins and associated genes (Arendt 2001; Arendt and Wittbrodt 2001; Arendt et al. 2004; Fernald 2006). We noted in Chapter 6 that chemoreceptive organs may have receptor cells that are ciliary (olfaction), microvillar (taste), or both (vomeronasal organs). And as discussed in Chapter 7, mechanoreceptors can rely on either of two widely distributed but distinct stimulation mechanisms, each having its own depolarizing ion (calcium or sodium), ion channel proteins (TRP or degenerin/ENaC), and associated genes. For each modality, the two alternative mechanisms seem to be equally ancient in the animal lineage. Why should most sensory modalities have evolved two

alternative ways of doing the same thing? While there may be differences in sensitivities of the two alternatives in any given modality, the same receptor cells never seem to employ both mechanisms: if the dual alternatives are present in the same organism, they are invariably assigned to different kinds of cells in different parts of the body. There is clearly more to the story of when and why cilia are recruited as sensory receptors that remains to be discovered.

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Web Topic 7.2

Hydrodynamic stimuli

Introduction

Hydrodynamic stimuli are created when an object moves through a fluid or a fluid moves past an object. The geometries of the stimuli and their persistence after being created vary with the size of the object, the relative velocities of the fluid and object, and the viscosity of the fluid. Although this sounds like a simple relationship, increasing one or more of these parameters do not simply scale up the stimuli, but instead can produce discrete changes in their geometries and life times. Fluid hydrodynamics turns out to be a fairly complicated area of physics. It is not an esoteric topic, however, as it is crucial to our understanding of weather patterns, the design of airplanes, helicopters, and sailboats, the mechanisms by which aquatic invertebrates and fish swim and birds, bats, and insects fly, the shapes of pine cones and flowers, the formation of spiral galaxies, and the behavior of black holes in space.

Reynold's numbers

Although the interaction between fluids and objects can produce quite varied hydrodynamic stimuli, molecular fluids such as air or water behave similarly once the appropriate scale corrections are made. This scaling is achieved by computing a dimensionless Reynold's number for the situation. The magnitude of the Reynold's number allows us to provide at least a qualitative prediction about what kinds of hydrodynamic stimuli will be created by the interaction of an object and a fluid when they are moving at different velocities.

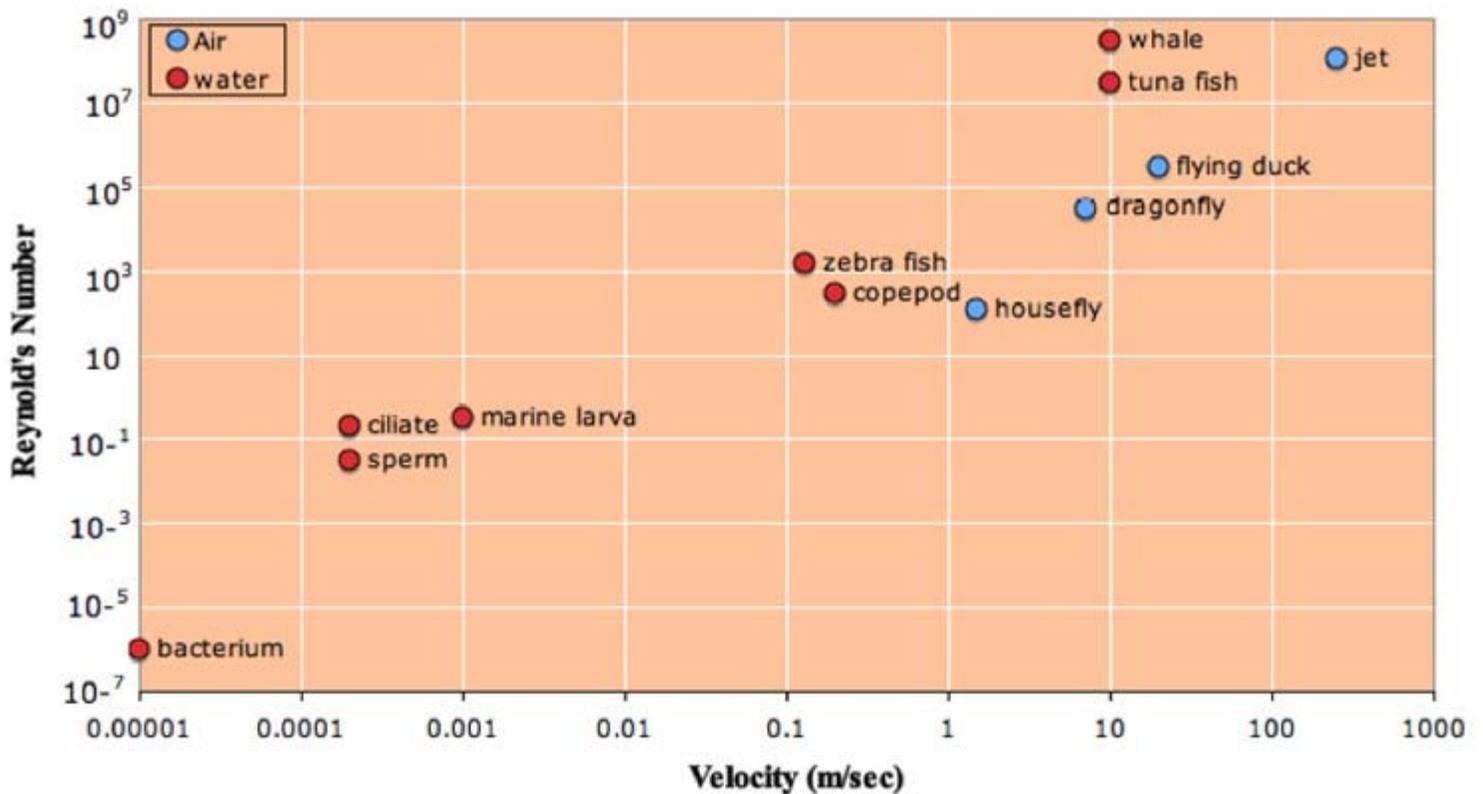
As discussed in [Web Topic 6.4](#), the Reynold's number is a ratio of the inertial forces in a fluid (which tend to maintain movement of the fluid) to viscous forces (which tend to slow down fluid movements). It is computed as the product of the **effective size** L of an object (in meters) and the **relative velocity** v of the object and the fluid (m/sec) divided by the **kinetic viscosity** of the fluid (m^2/sec). The latter is a measure of the resistance of a fluid to spreading at the ambient temperature. It is computed by dividing the **absolute (dynamic) viscosity** of the fluid μ , (the forward momentum of a given area of moving fluid measured in Newton-seconds/ m^2) by the **density** of the fluid ρ (kg/m^3). Algebraically, the Reynold's number, Re is thus equal to

$$Re = \frac{\rho v L}{\mu}$$

Water versus air

The density of water at room temperature is about 800–900 times that of air. The absolute (dynamic) viscosity of water is about 51 times higher than that of air. As a result, the same relative velocity of fluid and object and the same object size result in a Reynolds number in water that is about 15–17 times higher than that in air. Put another way, we expect air and water to show similar hydrodynamic behaviors when either the object or the flow rate (or more accurately, their product) is 15 times smaller in water. In practice, typical flow rates in air (e.g. wind) are 10–15 times faster than in water (e.g. stream currents). Animals of similar size in air and water thus tend to experience similar patterns of hydrodynamic stimuli (Vogel 1994).

Some examples of Reynold's numbers for moving objects in air (blue) and water (red):



Characterizing hydrodynamic stimuli

Hydrodynamic stimuli are traditionally generated by inserting an object of interest into a steady and linear flow of fluid. Wind tunnels are often used for studies with air, and water sluices for aquatic studies. In more recent studies, live animals are allowed to move through a static fluid (air or water), and the hydrodynamic effects of these movements studied. In either case, the challenge is to make visible the resulting eddies, vortices, and other movements of the fluid. Ideally, one would track the path of an individual fluid particle over time, and then repeat this effort with additional particles that began at different initial locations in the fluid. When no object is present in a steady fluid flow, each such particle should trace out a parallel straight line as it flows through the tunnel or sluice. These trajectories are called **pathlines**. Placing an object in a fluid flow will distort what otherwise would be straight and parallel pathlines. It will also create a mosaic of locations in front, around, and downstream from the object where fluid pressures and fluid velocities (both magnitude and direction) differ from each other and from the average for the fluid as a whole. Movement of an animal in a static fluid has similar effects. How can these be characterized?

There are a number of ways to visualize hydrodynamic perturbations in fluids (http://en.wikipedia.org/wiki/Flow_visualization). Several currently popular methods include:

- **Thread tracking:** Position fine threads in a grid and use their shape and/or direction pointed by their free ends to map the local patterns of fluid motions.
- **Particle tracking** (http://en.wikipedia.org/wiki/Particle_image_velocimetry): Add smoke, dyes, fine oil vesicles, tiny beads, or other particles to the flow and use visual recording methods to a) map areas of higher or lower concentration of the markers, or b) track the trajectories of individual particles over time (Yen & Strickler 1996; Videler et al. 1999; Hanke et al. 2000; Videler et al. 2002; Hanke & Bleckmann 2004; Videler 2005; Catton et al. 2007; Schulte-Pelkum et al. 2007).
- **Schlieren optics** (<http://www.fas.harvard.edu/~scidemos/LightOptics/SchleirenOptics/SchleirenOptics.html>): Heterogeneity of density and velocity in the fluid produces heterogeneity in its refractive properties. Light is passed through the fluid and local differences in refractive index produce an image with correspondingly lighter

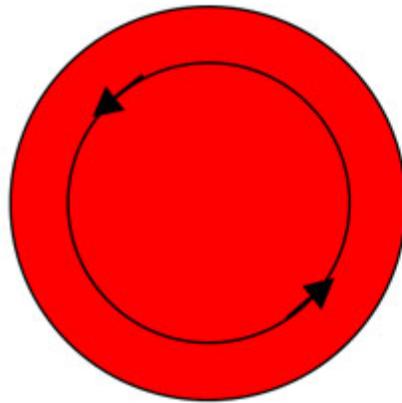
or darker regions (Hwang & Strickler 2001).

- **Laser Doppler Anemometry** (<http://www.aoe.vt.edu/~devenpor/aoe3054/manual/expt4/index.html>): Light from a single laser is split into two beams emanating from different points but focused by a lens on a common point. When a reflective particle being moved in a fluid flow passes through this focal point, the two beams are reflected slightly out-of-phase depending upon the velocity and direction of movement of the particle. The reflected beams are recombined and the velocity of the particle is computed based on the level of beam interference (Bleckmann et al. 1991).

Vortices

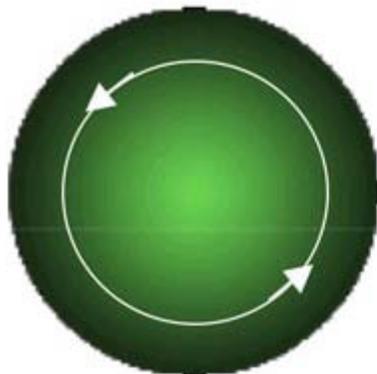
When water in a flowing stream encounters an obstacle, the result is often a swirling eddy. Eddies are one example of a vortex. In a vortex, pathlines become circular or spiral instead of linear or gently curvilinear. There are several kinds of vortices:

- A **rotational vortex** is one in which all contents within the vortex rotate around the central axis at the same angular velocity. Imagine a pan of water placed on a round turntable. A point a short distance from the center of the resulting vortex will move over a shorter curvilinear distance in a given time interval than will a more distant point. While angular velocity (complete circuits/sec) is the same everywhere,



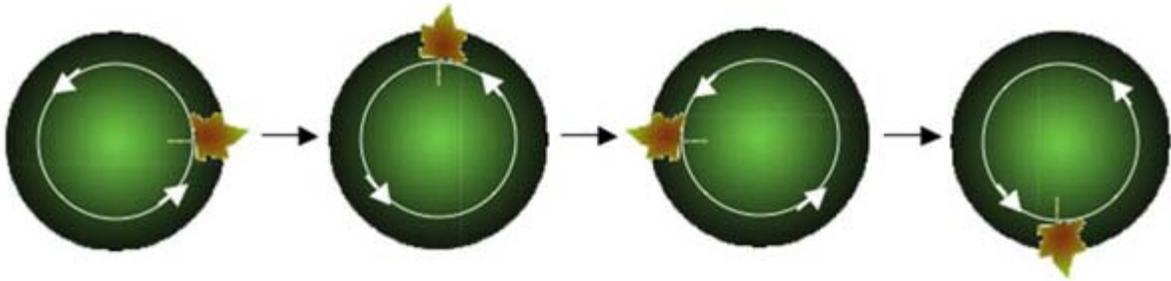
Angular velocity
(same everywhere)

more peripheral points in the vortex travel at a higher curvilinear (tangential) velocity than do more central ones:

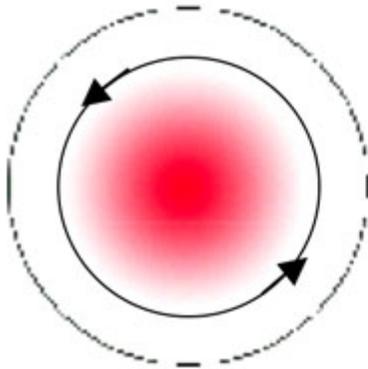


Curvilinear
(tangential) velocity
(darker color is faster)

Suppose a leaf falls onto the right side of a rotational vortex with its twig end closest to the vortex center and its tip facing the periphery of the vortex. Because the tip end of the leaf will move faster in a curvilinear trajectory than the stem end, by the time the leaf gets to the left side of the vortex, the stem end will now point to the right (still towards the center of the vortex), whereas the tip end will point left (towards the periphery). Thus an object borne by a rotational vortex will rotate about its own axis as it moves around one full circuit of the vortex.

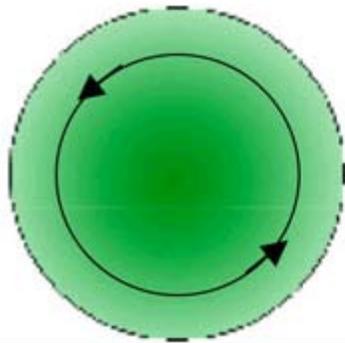


- An **irrotational vortex** also rotates around a central axis, but points closer to the center have a higher angular velocity than do more distant points:



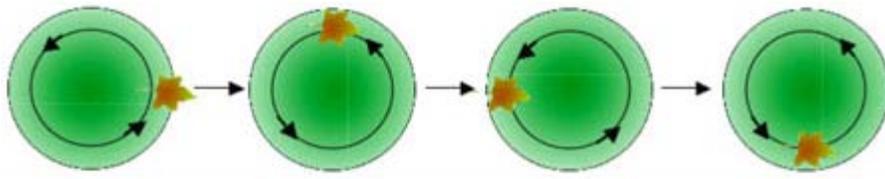
Angular velocity
 (darker red shows higher velocity; angular velocity decreases as inverse of square of radius)

We can create such a vortex by putting a spinning beater or cylinder into a pan of water. Water closest to the spinning object will have the highest angular velocity, while more distant regions of water will rotate around the pan more slowly. And here, the tangential velocity is also higher near the center:



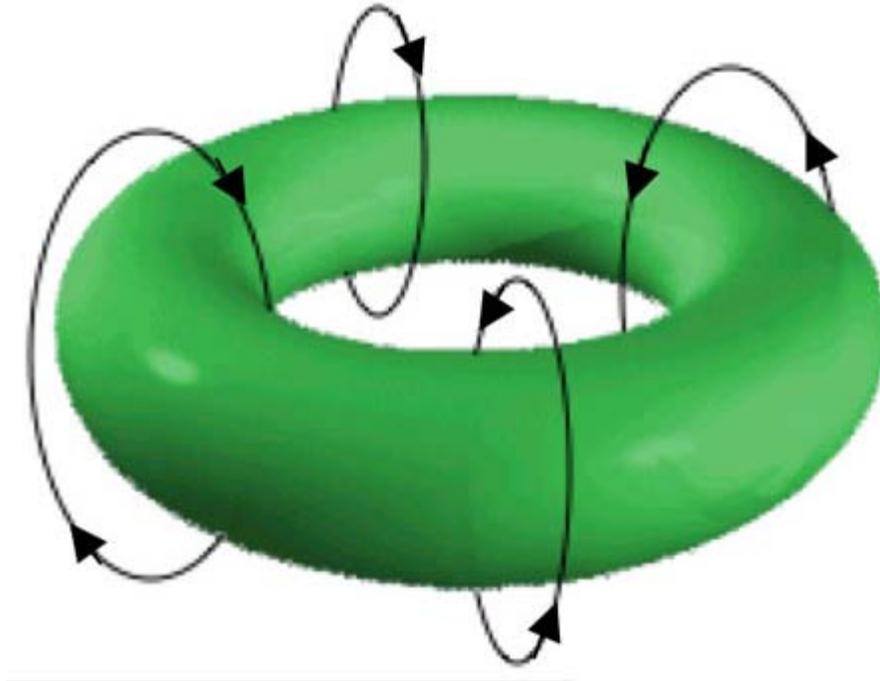
Tangential velocity
 (darker green shows higher velocity; tangential velocity decreases as inverse of radius)

In fact, the product of tangential velocity and radius will be a constant. Suppose a leaf drops into the right side of this vortex with its stem aimed towards the center and its tip towards the periphery. As it rotates around the pan, its stem will move more quickly along its circular path than will the leaf tip move along its path. The result is that the leaf will continue to have its stem aimed to the left as it moves around the vortex; it does not rotate around its own axis as in a rotational vortex.



Hence the name “irrotational” vortex.

- A third example is called a **vortex ring**. Here, the vortex takes the shape of a doughnut (torus):



Fluid circulates around the cross-section of the torus such that all fluid entering the center of the torus from a given side is going in the same direction. The result is a “jet” of fluid moving through the torus center parallel to its axis. A cross-section of the torus would thus show the direction of circulation to be opposite on opposing segments of the torus. This has to be the case if all fluid passing through the center is going in the same direction. A smoke ring is a well-known example of a torus. Vortex rings are usually moving as a whole along a line parallel to their main axis while passing fluid circulates through the center and around the periphery to enter again on the opposite side.

- **Complex and multiple vortices:** Most irrotational vortices actually contain a rotational vortex at their core and thus are a combination of the two types. Although it is possible to generate a single vortex (e.g. when water or air flows over the ground and encounters a hole or trench in the surface inside of which a vortex is often created), most vortices are created in pairs (rotational and irrotational vortices) or even larger numbers of the same kind of vortex (ring vortices). Pairs of vortices created at the same time usually rotate in opposite directions. Persistent vortices circulating in opposite directions tend to repel each other; those circulating in the same direction will attract each other and may fuse into one larger vortex. Note that vortices do not need to be planar. In fact, many are three dimensional. Examples of three dimensional vortices include water circulating around and through an open drain, tornadoes, dust devils, some kinds of waterspouts, and hurricanes and cyclones. Large animals moving in fluids tend to produce strings of successive ring vortices as a **wake** behind them. These tend to be aligned such that the jet passing through one is continuous with the jet passing through the one created before it and the one created just after it.

Examples of naturally occurring vortices can be found online at <http://www.engineering.uiowa.edu/fluidslab/gallery/vortex.html>.

Boundary layers

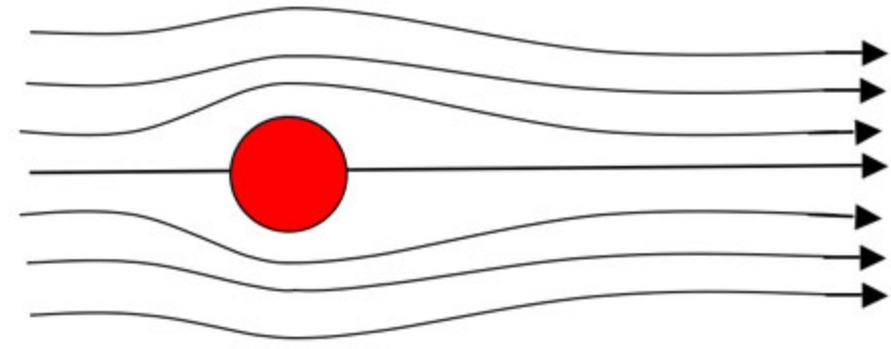
When a volume of fluid and a solid object are moving relative to each other, those molecules of fluid closest to the object surface cannot move differentially from the object. They are forced to move with the object and thus act as if “stuck” to the surface. Fluid molecules far enough away from the object will move at the same relative velocity as other nearby molecules of the fluid volume. In between, there is a gradient of relative fluid velocity which goes from zero at the object surface to that shared by most of the molecules in the fluid volume. This intermediate region showing a gradient of velocity around the object is called the **boundary layer**.

As fluid slows down and collects in a thin boundary layer on the upstream side of an object, molecules that are not too close to the surface flow along pathlines that track the surface shape of the object. At some point along each side of the object's surface, this fluid stops following the object shape and simply heads off downstream. These are known as the **separation points**. For very low Reynold's numbers, the separation points are located well on the rear (downstream) side of the object. As Reynold's numbers are increased, the separation points move forwards toward the object's upstream side. This allows an increasing amount of fluid to pool on the downstream side of the object where it can even backflow towards the object, move along lines parallel to its surface, and finally join the downstream flow at the separation points. This circular movement thus generates eddies or vortices downstream from the object. At high enough Reynold's numbers, the separation points detach from the object and move downstream. This drastically changes the composition and properties of the downstream boundary layer.

Patterns of hydrodynamic stimuli

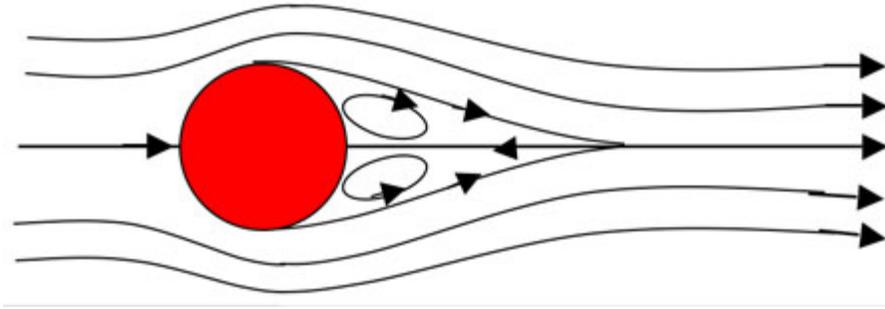
Consider a static object in a continuous flow of fluid. As noted above, low Reynold's numbers are obtained when the kinematic viscosity is much greater than the product of relative velocity and object size. Put another way, the resistance of the fluid to spreading in this case exceeds the inertial forces imposed on the fluid by its encounter with the object. When the object is large and/or the relative velocities are high, then inertial forces easily exceed the viscous resistance of the fluid. This is the case for large Reynold's numbers. Intermediate values result in a more even match between viscous and inertial factors. Depending on the relative influences, there are also two intermediate cases that are easily distinguished. Each of these four situations generates a qualitatively different type of hydrodynamic stimulus (Cf. Feynman 1964 and Vogel 1994):

- **Very Low Reynold's Numbers (<10):** These conditions produce unidirectional flow of the fluid despite the presence of the object. Either the object is so small or the relative velocity of object and fluid so minimal that pathlines that would otherwise intersect the object are bent so that the fluid simply sweeps past the object without causing eddies or other effects:

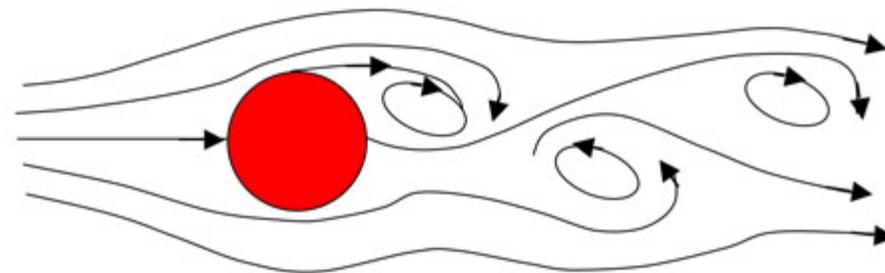


The viscous forces in this situation quickly attenuate any perturbations in the fluid as heat. No vortices are formed. In the case of a fish in water or insect in air with such a low Reynold's number, the passage of the animal leaves no detectable wake to the side or downstream from it.

- **Low Intermediate Reynold's Numbers (10–50):** With larger objects and/or higher relative velocities between fluid and object, fluid begins to pile up on the upstream side of the object faster than it can flow around the object to relieve the pressure. As it works its way around the object, it creates eddies (vortices) on the downstream side. The typical result is a pair of vortices circulating in opposite directions and remaining "attached" (e.g. fixed in location relative to the object).



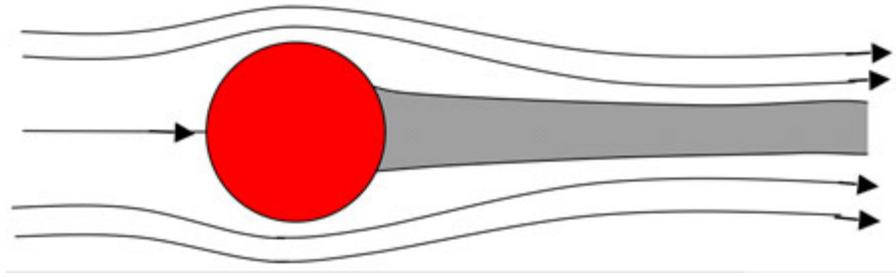
- **High Intermediate Reynold's Numbers (50–200,000):** With still larger objects or higher relative velocities, the generated vortices become very large and are “shed” into the downstream fluid. Instead of two attached vortices at any time, a single vortex forms downstream from the separation point on one side of the object until it is shed, and then a second vortex forms with the opposite circulation pattern behind the opposite separation point. The two sides of the object thus alternate in creating shed vortices. The result is two parallel trails of downstream vortices called a **von Kármán vortex street**:



For animations of a von Kármán vortex street see Wikipedia (<http://en.wikipedia.org/wiki/File:Vortex-street-animation.gif>) and for photos of naturally occurring examples see Weather Vortices (<http://www.weathervortex.com/wakes.htm>).

The regular frequency with which an object sheds successive vortices can be computed from another dimensionless parameter called the **Strouhal number**. This depends on the size of the object and the relative velocity of object and fluid. Shed vortices are usually ring vortices and successive vortices in the same track typically share a common jet (Videler et al. 2002). Note that while relative flow velocity sufficiently downstream from the object is relatively constant everywhere at low Reynold's numbers, shed vortices produce very heterogeneous velocity profiles downstream of the object over a wide area and for as long as the vortices continue circulating. Since inertia greatly exceeds viscous resistance, vortices can persist for many minutes after a swimming or flying animal has moved on. These heterogeneities in velocity and fluid pressure can feed back on the object and make it vibrate in synchrony with the frequency of vortex generation. If this frequency is close to a resonant frequency of the object, significant vibrational amplitudes are possible. The interactions of both attached and shed vortices and the objects producing them are exploited by many animals and humans to facilitate flight, swimming, feeding, and other functions (Webb 1978; Vogel 1994; Videler 2005). As Reynold's numbers increase, the orderly arrays of shed vortices become increasingly disordered by turbulence. Initially, this turbulence is confined to the regions inside each vortex, but at even higher Reynold's numbers, even the vortices are disrupted by turbulence in the fluid.

- **High Reynold's Numbers (>200,000):** At a sufficiently high Reynold's number, the value of which depends largely on the object shape, the separation points for flow around the object separate from it and move downstream. This drastically reduces the drag experienced by the object and narrows the downstream boundary layer to a much smaller “tail” behind the object. Within that boundary layer, structured vortices are usually absent. Instead, the content is unstructured turbulence and chaos.



Animal wakes

Animals that move through water or air are more likely to leave behind a persistent wake if they are large and/or they move quickly. A small copepod that is slowly foraging may leave no wake at all; however, if it is startled and leaps away, it is likely to leave behind some shed vortices that could be detected by an appropriate predator (Yen & Strickler 1996; Videler et al. 2002). The higher the relevant Reynold's number, the more likely a wake will be left behind and the longer it will persist (Vogel 1994). As noted above, the spacing and persistence of shed vortices could provide information about the size and velocity of the animal creating them. The situation is complicated by the fact that most animals achieve locomotion by repetitively moving some body part: birds and insects flap their wings, copepods oscillate paired appendages, and fish undulate. The frequency composition of persistent wakes can then also be used to extract additional information about the wake's creator (Bleckmann et al. 1991).

Further Reading:

There are a number of texts that cover hydrodynamics and fluid mechanics. In order of increasing mathematical difficulty, we recommend: Vogel (1994) (an outstandingly readable treatment of fluid dynamics, vortices, and hydrodynamics from a biologist's point of view. Strongly recommended!); Videler (2005) (This book focuses on animal flight, but provides a useful general introduction to Reynold's numbers and vortices); Feynman (1964) (chapters 40–41 outline the basic logic of fluid mechanics. The book uses vector math, but Feynman is so good at explaining things that a reader need not be fully fluent with curls and gradients); and Lighthill (1986) (despite the title, this is a more advanced text using the usual vector math associated with fluid mechanics. It is widely cited in the prior books.).

Some published articles on biological aspects of hydrodynamics include Bleckmann et al. 1991; Blickhan et al. 1992; Catton et al. 2007; Dehnhardt et al. 2001; Hanke et al. 2000; Hanke & Bleckmann 2004; Jiang & Osborn 2004; Kim & Choi 2007; Liu et al. 1998; Magnuson 1978; Müller et al. 2000; Müller et al. 2002; Pohlmann et al. 2001; Schulte-Pelkum et al. 2007; Sun & Tang 2002; Webb 1978; and Yen & Strickler 1996.

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Web Topic 7.3

A primer on electrical signals

Basic electrostatics

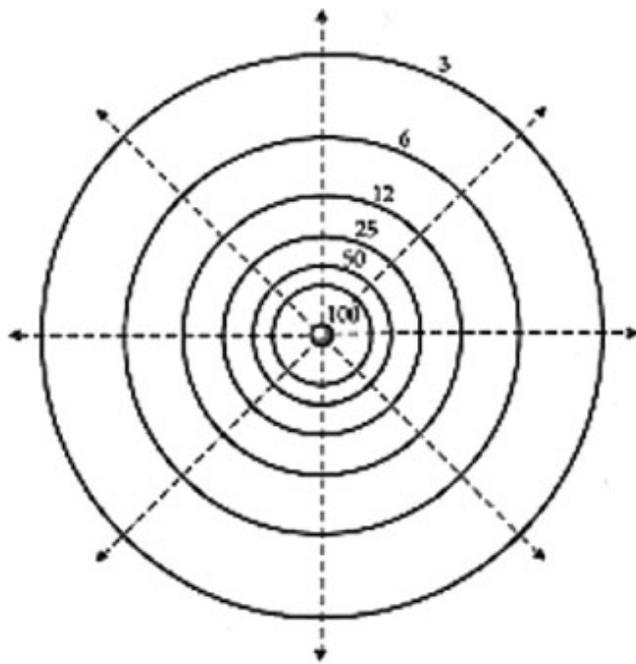
- **Charge:** An object (atom, molecule, piece of material containing many molecules) with unequal total numbers of electrons and protons is said to be **charged**: each excess electron adds a charge of -1 and each missing electron (excess proton) adds a charge of +1. The net charge on the object is the sum of the charges contributed by each unpaired electron or proton. It is usually measured not in electrons or protons but in **coulombs**. One coulomb is equal to 6.25×10^{18} unpaired electrons (or protons).
- **Coulomb's Law:** Two nonmoving objects in a vacuum with charges Q_1 and Q_2 respectively will be attracted to each other (if Q_1 and Q_2 have opposite signs) or repelled (if Q_1 and Q_2 have the same sign) with a force F (in **Newtons**) equal to:

$$F = \frac{1}{4\pi\epsilon_0} \frac{Q_1 Q_2}{r^2}$$

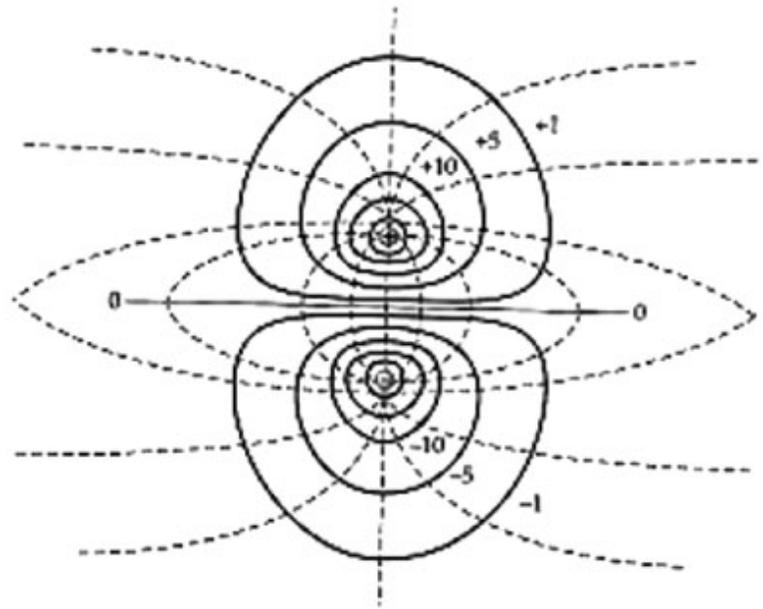
where r is the distance between the two objects in meters, and ϵ_0 is known as the **permittivity constant** ($= 8.85 \times 10^{-12}$ coulombs²/newtons•meters²). Note that the amplitude of this force decreases with the square of the distance. It thus can become quite weak at large distances from the object.

- **Electric Field:** A small test charge moved into any location near enough to a charged object will experience a net electrostatic force. A map of the direction and amplitude of that force at all locations around a charged object defines the **electric field** around the object. For a single charged object (**monopole**), the electric field lines of force radiate away from (or towards) the object equally in all directions. If multiple charged objects are present, the amplitude and direction of the net force at any point in the electric field is the vector sum of the component forces present at that point. For two charges of opposite polarity (sign) sufficiently close together (a **dipole**), the lines of force in the surrounding electric field are curved.
- **Multipolar Fields:** The electrical fields generated by biological sources are rarely dipolar and practically never monopolar. Instead, complex arrays of charges will generate many axes around which the charges are distributed. The resulting electrical field is the sum of the effects of the multiple axes. The most important axis is usually the dipole component, the next most important axis the quadrupole component, a third axis the octupole component, etc. The relative contributions of each axis to the overall electrical field depends on the distance between the sampling point and the object. Dipole contributions fall off with distance as $1/r^3$, quadrupoles as $1/r^4$, octupoles as $1/r^5$, etc. As a result of the faster fading of higher order axis contributions, only the dipole component will be detectable at large distances; however, at close distances, all components can contribute significantly to the electric field.
- **Electric Potential:** The electrostatic **potential** at any location surrounding a charged object is the amount of work that is required to bring a small unit of positive charge from infinity (where the electric field force surrounding the object is zero) to the location. If the object has an overall positive charge, one must do work against the field's repellent force to bring the unit charge to the location. The electrostatic potential in this case is said to be positive. If the object has a negative charge, it will exert an attractive force on the positive test charge and thus the work done to bring the test charge closer will be negative. In this case, the electrostatic potential at the final resting location of the test charge is said to be negative. Electric potential is measured in **volts** and is thus often called the "voltage" at a location. The electric field is the spatial gradient in voltage at any location. The potential difference between any two points in the electric field is simply the difference between the voltages at the two points and is often called the "voltage drop" between the two points. One can connect all points around an object that have the same voltage as isopotential lines. These are equivalent to the lines connecting all locations at the same altitude in a topographic map. Examples of the electric field lines (dashed) and isopotential lines (solid) for a monopole and a

dipole are shown below:



Monopole



Dipole

- **Dipole Voltage:** The voltage V at a distance r from a dipole and an angle θ (relative to the line joining the two point charges in the dipole) is

$$V(r, \theta) = \frac{1}{4\pi\epsilon_0} \frac{Q\delta\cos(\theta)}{r^2}$$

where Q is the magnitude of the charge on each part of the dipole and δ depends on the distance between them. Thus along the line perpendicular to that joining the two charges and midway between them, the angle θ is 90° and the $\cos(90^\circ) = 0$; thus the voltage along that line is zero. Points outside the dipole but along the line joining the two charges will show the maximal voltage values.

Electric fields in different media

- **General Formulation:** The formula given above for the electrical force at any location surrounding two charges Q_1 and Q_2 in a vacuum can be generalized for two charges in any medium as follows:

$$F = \frac{1}{4\pi k\epsilon_0} \frac{Q_1 Q_2}{r^2}$$

where all terms are as before and k is the **dielectric constant** of the medium. A vacuum is a perfect **insulator** in that the electric force created by the two charges cannot induce any repositioning or movement of other electrons, atoms, or molecules. The dielectric constant for a vacuum is 1.

- **Conductors:** At the other extreme, are **conducting** media in which electrons, atoms, and/or molecules are present and free to move under the influence of the electric field. Moveable electrons, for example, in the presence of an electric field will move towards the positive pole leaving their formerly paired positive charges to accumulate near the negative charge. This redistribution of elements of the medium so that opposite charges accumulate around the initial charges continues until it cancels out the electric field inside the conductor. The dielectric constant for a

conductor is thus set at infinity, and plugging this value into the above equation, one can see that inside the conductor, the force at any location is zero. By the same token, it will take no work to move a test charge around inside the conductor and thus the voltage inside a conductor is the same everywhere.

- **Dielectrics:** These are media in which movements of electrons, atoms, and molecules are constrained. However, it is still possible for electrons to move within a medium atom or molecule, or it is possible for a molecule to rotate so that its most positive side faces the negative charge and its negative side faces the positive charge. The parallel alignments of medium molecules or electrons inside an atom or molecule create thousands of tiny dipoles with lines of force opposite to those surrounding the original charges. The result is a reduction in the amplitude of the electrical field surrounding the charges: greater polarization of the medium results in greater diminution of the electrical field. Higher values of the dielectric constant reflect greater susceptibility to polarization and thus a greater reduction in the electrical field inside the medium. The dielectric constant for air is 1.00054, glass 4.7, and freshwater at room temperature about 80. Note that the dielectric constant also affects the measurable voltage at any point inside the medium. For example, the electrical potential surrounding a dipole in a non-conducting but dielectric medium is:

$$V(r, \theta) = \frac{1}{4\pi k \epsilon_0} \frac{Q \delta \cos(\theta)}{r^2}$$

Electric currents

- **Ohm's Law:** Suppose we place an electric dipole in a medium which is a worse conductor than a metal, but a better conductor than most dielectrics. Water is such an example. Water invariably has dissolved materials within it, and many of these, such as salts, break up in water into their component charged ions. The presence of an electric field in water will cause positive and negative ions to move in opposite directions. The ionic trajectories follow the electric field lines. This movement of ions in water (or of electrons in a metal) is called an **electric current**. The magnitude of an electric current between two points (measured in coulombs/second or **amperes**) is proportional to the voltage difference between the points. The constant of proportionality between an applied voltage and a resulting current is called the **conductance** of the medium through which the current is flowing. More often, we use the reciprocal of conductance which is called the **resistance**. If V is the voltage difference between two points and R is the resistance (in **ohms**), then the current I (in amperes) depends on these variables according to Ohm's Law:

$$I = \frac{V}{R}$$

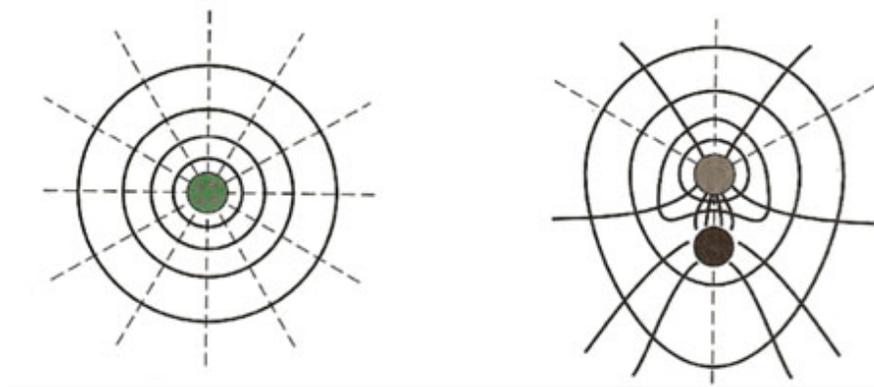
The convention in physics is that current flows from a region of positive voltage to one of more negative voltage. Note that this is opposite to the actual flow of electrons in a metal (from a negative to positive potential location).

- **Resistivity:** Resistance in a particular context will be higher the greater the distance that the current must flow, the smaller the cross sectional area through which the current passes, and the worse the material as a conductor. The latter term is characterized by the material's intrinsic **resistivity**. Because of the resistance of the water in which we have placed our dipole, there will be a steady current of ions towards that part of the dipole of opposite charge to each ion. If there were no resistance, the initial current would quickly cancel the charge at each end of the dipole due to accumulations of oppositely charged ions. If the resistance is high enough, it may take some time before the dipole is fully neutralized. Alternatively, something may occur near the dipole to restore its charge. In either case, if the electric field is maintained or restored for a sufficiently long period, we can measure the electric potential at various points around the dipole and the amount of current at each location. For a stable source of current in a conducting medium, the potential at location (r, θ) from the dipole is

$$V(r, \theta) = \frac{\rho_0 I \delta \cos(\theta)}{4\pi r^2}$$

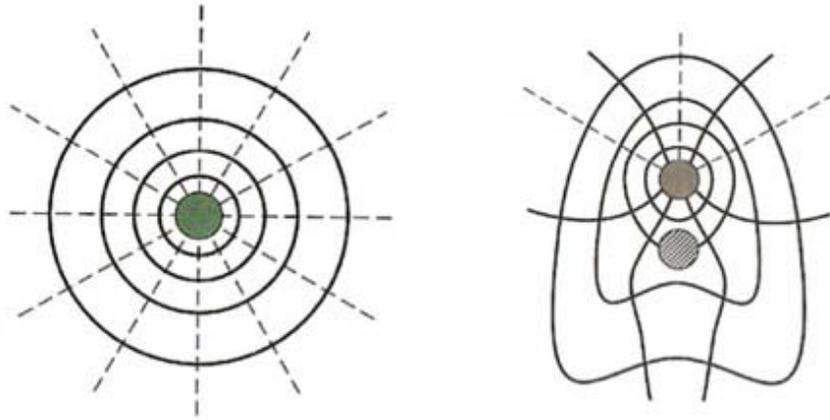
where the medium resistivity, ρ_0 and the current I have replaced the permittivity, $k\epsilon$, and the charge, Q , used for non-conducting media.

- Varying Electric Fields and Impedance:** Water and many other materials are both conductors and dielectrics: some current will flow through them, but the resistance is high enough that electric fields are sustained and their ability to be polarized and act as a dielectric permits some build-up of counter-fields within the medium. For static electric fields, this may not be significant. If however, the electric field is changing in magnitude or direction, then the dielectric properties of the medium can become important. In a steady electric field, an electron in a conductor may move the entire length of the conductor. This is called a **direct current (DC)**. Now suppose we apply a sinusoidally varying electric field to the conductor. Electrons will first move one direction and then back the other. This is an **alternating (AC)** current. The higher the frequency of the alternating field, the less distance any one electron can travel before it has to turn around and go the other way. In a non-conducting dielectric, electrons or polar molecules can move a bit, but they can never move far enough to sustain a steady DC current. However, if an alternating field is applied across such a material, the distance electrons have to travel per cycle may be within the polarizing limitations of the material: the higher the dielectric constant for the material, the slower the frequency of alternation which the material can track and thus carry current. The effective resistances of dielectrics may thus drop if the applied electric field is a varying one. To keep this notion of resistance distinct from classical DC resistivity, the term applied to such dielectrics is **capacitive reactance**. Capacitive reactance decreases with the dielectric constant of the material and with the frequency of the electric field oscillation. Like resistance, it is measured in ohms. Remember that even if the waveform of the electric field variations is not sinusoidal, it can be considered as the sum of a number of different sinusoids (see [Web Topic 2.4](#)). Applying such a non-sinusoidal signal to a dielectric, we will find that the dielectric will act like a high-pass filter since it can more easily track the higher frequency components than the lower frequency ones. The overall **impedance** of a medium like water to a varying electrical field will thus depend on both the resistivity of the water and on the capacitive reactance of the water at the various frequencies making up the waveform of the changing field.
- Electrical Field Distortion:** We have assumed so far that media are unbounded and homogeneous. The resulting electric fields can be called **free fields** (by analogy with sound). However, most media have boundaries and contain objects whose dielectric and/or resistive properties differ from those of the medium. The usual situation is thus not a free field. Boundaries and objects in the medium will distort and change the field shape from free field conditions. For example, suppose we place a monopole in a medium such as water (left figure below) and then place an objects with a resistivity less than water near to the charge (right):



Objects which have lower resistivities than the medium bend the electric field lines in the region between themselves and the charge closer together and towards the object. This region of enhanced electric field magnitude corresponds to a region of very closely spaced isopotential lines and thus a steep gradient in voltage. Objects which have higher resistivities than the medium (below right) bend the electric field lines away from themselves, lowering the field magnitude in the region between themselves and the charge, and show a flattening

of the potential gradient in this region:



When many objects of differing conductivities are present, the shape of the field can become highly complex. Boundaries are also significant. If we place our charge near to the air-water interface, or near a non-conducting bottom, the electric field magnitude and potential near to the charge will be twice as great as that for a charge suspended in an unbounded volume of water. This is because current can radiate in all directions in the unbounded case, but can only radiate away from the water's surface in the bounded example.

See Chapter 7 for examples of how differential resistance and capacitance in nearby objects can be used by some electric fish to discriminate between prey and inedible items, and to navigate through familiar locations.

Web Topic 7.4

Bioelectric field resources

Introduction

A variety of fish and a few primitive mammals have receptors that can respond to the electrical fields generated by other animals and electrochemical habitats. A subset of the fish species have also evolved special organs that can create significant electrical fields on command and invoke these electrical organ discharges for electrolocation and communication.

Passive electroreception

- **Paddlefish swimming:** This YouTube video gives a good view of paddlefish swimming:
<http://www.youtube.com/watch?v=fysqA0tr4qo>
- **Sharks, rays, skates, sturgeon coelocanths, and echidna:** Good still images and/or movies of these passive electroreceptive animals can be found at: <http://www.arkive.org/>. The video of the thornback skate includes a brief look at its underside where the electric system pore openings can be seen (<http://www.arkive.org/thornback-skate/raja-clavata/video-00.html>)

Active electrogeneration and electrolocation

- **Phil Stoddard Lab** (Florida International University): This group has measured the electric fields (as voltages) around various electric knifefishes (*Gymnotiforms*) and reconstructed the temporal variation in these fields as Quicktime movies:
http://www.fiu.edu/~efish/visitors/electric_field_animations.htm
- **Mark Nelson Lab** (University of Illinois, Urbana-Champaign): This site contains a series of very helpful webpages including movies and animations of electric fish foraging. Suggested links:
 - Background on electric fish:
http://nelson.beckman.uiuc.edu/electric_fish.html
 - Background on electrolocation:
<http://nelson.beckman.uiuc.edu/electrolocation.html>
 - Movies of foraging electric fish including simulations of stimulus patterns:
<http://nelson.beckman.uiuc.edu/movies.html>
- **Malcolm MacIver Lab** (Northwestern University): This group uses simulation and robotic models to study the stabilizing movements and electrical field measurement by electric fish. Additional programs may need to be downloaded to view some of these models and simulations:
<http://www.neuromech.northwestern.edu/uropatagium/-RoboVid>
- **James Bower Lab** (California Institute of Technology): This group, including Chris Assad and Brian Rasnow, created a number of movie simulations of the electric fields of discharging fish. Pages include:
 - Electric fish Quicktime movies:
<http://alumnus.caltech.edu/~rasnow/index.html>
 - Electric fish field simulations:
<http://alumnus.caltech.edu/~rasnow/sim.html>
 - Responses to stimulation:
<http://alumnus.caltech.edu/~rasnow/behav.html>

Electrocommunication

- **Carl Hopkins Lab** (*Cornell University*): Dr. Hopkins and his colleagues have posted a Flash movie of a spectrogram of electrical signaling with annotations. This example is typical of such interactions in electric fish. Be sure to listen to this file when you play it:
Knifefish (*Sternopygus macrurus*): male courting female:
http://www.nbb.cornell.edu/neurobio/hopkins/sternopygus/sternopygus_singing.htm
- **Erik Harvey-Girard**: This site (in French) has a very nice review of electrocommunication in the knifefish, *Apteronotus*: <http://www.apteronote.com/>. Use the directory on the left side of the Introduction page to examine various topics.

Other topics

- ***An Expedition to Africa in honor of Mary Kingsley's Prior Contributions to Electric Fish Biology:***
<http://www.nbb.cornell.edu/neurobio/hopkins/mkingsley.html>

Web Topic 7.5

Adaptations for passive electroreception

Introduction

The early acquisition of passive electroreceptors in primitive fish was surely a key adaptation that facilitated its subsequent radiation and eventual dominance in aquatic habitats. In both marine and freshwater habitats, a number of strategies are employed to enhance passive electroreception.

Variations in the spatial distribution of receptors

Spreading many ampullary organs (or teleost equivalents) over a large area of body surface allows an animal to sample the amplitude of the electric field at many locations. Because the walls of ampullary canals are highly resistive, little current passes into or out of the canal except along its major axis. Thus electric field lines parallel to a canal will produce the largest stimulation of the associated sensory cells. Comparisons of stimulus levels for canals with nearby pores but different axis angles thus allow the animal to estimate not only the strength of the electrical field at a location but also its direction there. Pooling of inputs from many organs then permits the animal's brain to generate a fairly accurate map of the electrical field surrounding the sampled body surface (Montgomery and Bodznick 1999; Brown 2002; Keller 2004; Bell and Maler 2005; Bodznick and Montgomery 2005). This map can be extremely useful in determining the location of the electric field source and whether it is moving relative to the sampling animal.

Whereas lampreys, lungfish, and several extinct taxa of primitive fish spread their electroreceptive organs over much of their body surface (Bodznick and Northcutt 1981; Northcutt 1986; Ronan 1986; Northcutt 1997; Watt et al. 1999), the majority of passively electroreceptive animals concentrate them in relevant regions of their heads (Northcutt 1986; Zakon 1988; Jørgensen 2005). Within the head region, the distribution of the organs and their associated pores varies with the species' habitat, diet, and light levels when foraging. Because ampullary organs develop from the same embryonic tissues as the lateral line, their distribution is also affected by the disposition of the animal's hydrodynamic canals and superficial neuromasts (Northcutt 1986).

The 400–2500 ampullary receptors of sharks are concentrated entirely on their heads (Bodznick and Boord 1986). Species that forage in open ocean tend to have a more even distribution of receptors over the head's dorsal and ventral surfaces while those that forage on benthic prey (such as skates) concentrate the receptors on the ventral side particularly around the mouth (Tricas 2001; Collin and Whitehead 2004). Sharks that feed on benthic prey as juveniles but in deeper waters as adults undergo a shift towards more even dispersion of ampullary receptors as they mature (Collin and Whitehead 2004). A more widespread distribution of receptors on the head would also facilitate the use of the earth's electric fields for migratory species, but whether sharks can actually use electroreception for long range navigation remains unclear (Kalmijn 1974, 1988; Klimley 1993; Paulin 1995; Sundstrom et al. 2001; Collin and Whitehead 2004; Tricas and Sisneros 2004; Wilkens and Hofmann 2005).

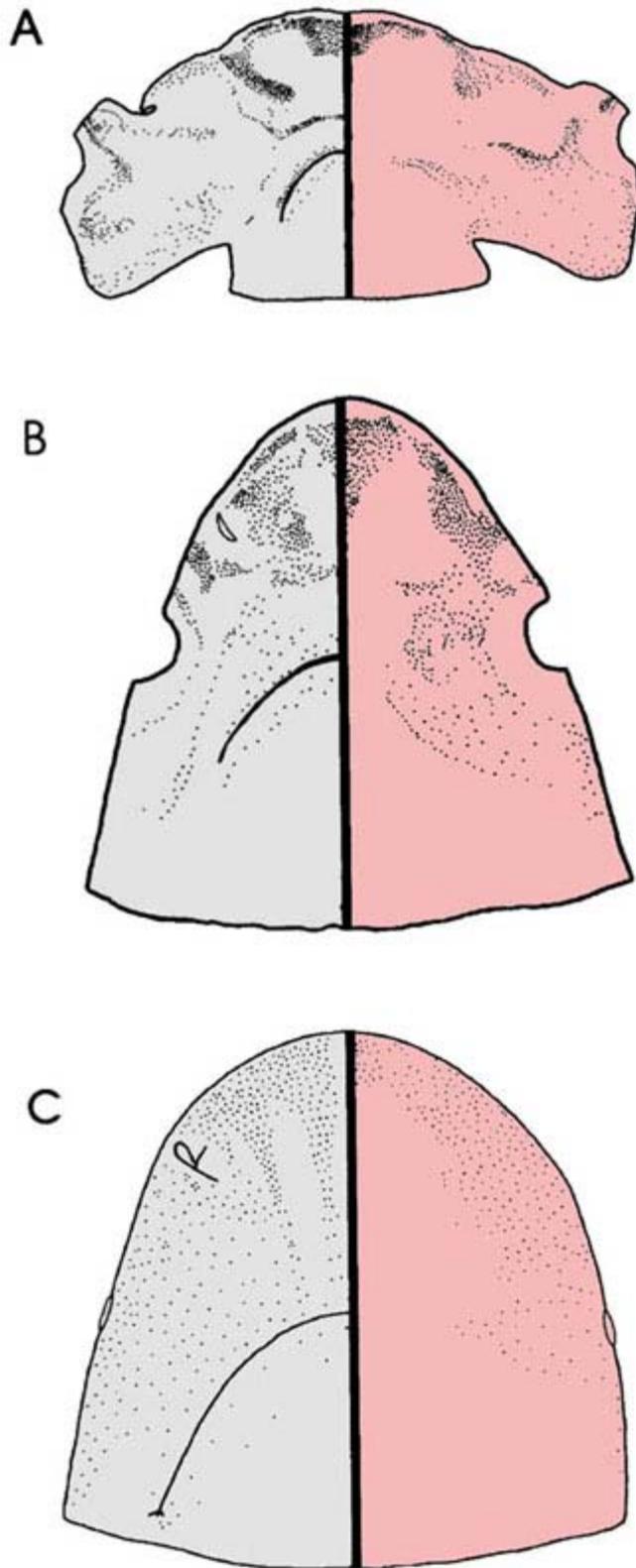


Figure 1. Distribution of ampullary organ pores on the heads of sharks as function of foraging habitats. Ventral view (left half), dorsal view (right half), and ampullary canal openings (dots) are shown in each example. A) Hammerheaded sharks (*Sphyrna spp.*) often feed just over the bottom of bays and estuaries, and young sharks live in murky waters with low visibility. Approximately 60% of their canal openings are on the ventral side of their bodies where prey are more likely to be encountered. B) Sandbar sharks (*Carcharhinus plumbeus*), like most shark species, have equal numbers of ampullary canal openings on the ventral and dorsal sides of the head. They encounter prey both above and below the body and can use vision to orient their attacks. C) Bull sharks (*Carcharhinus leucas*) are unusual in their ability to tolerate brackish and freshwater habitats with

limited visibility. Like the hammerheaded sharks, bull sharks concentrate nearly 60% of their ampullary canal openings on their ventral side ahead of and to the side of their mouth. (After Collin and Whitehead 2004.)

The head of a skate or a ray merges smoothly into the flattened wings on each side of the body. Adult skates and rays can have from 400–1400 ampullary organs depending on the species (Bodznick and Boord 1986). These are usually clustered around the head but radiate their canals in all directions including several long canals that open on the rear edges of the wings. As with sharks, species that feed on benthic prey have higher concentrations of receptors and canal pores on their ventral side and around the mouth, whereas larger species that pursue fish as prey have a more even distribution on the dorsal and ventral sides of their bodies (Bodznick and Boord 1986; Raschi 1986; Tricas 2001). Large pelagic species, such as the manta rays (*Myliobatidae*), have many fewer electroreceptors than shallow water forms and these are limited to small patches on their ventral side (Bodznick and Boord 1986).

Freshwater paddlefishes (*Polyodontidae*) feed on tiny (< 5mm) planktonic crustaceans such as *Daphnia*. Each fish sports a long flat rostrum on its head:

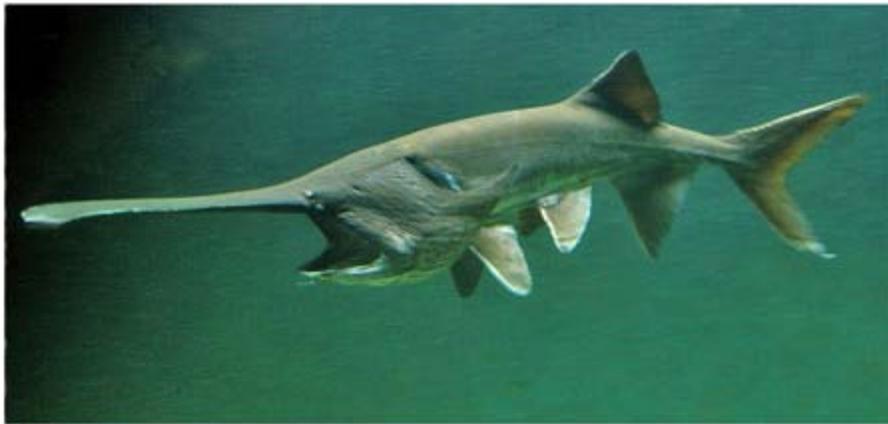


Figure 2. Photo of paddlefish (*Polyodon spathula*) foraging with mouth open. Paddle extends forward from head. (Photo by David Alexander.)

This rostrum is covered with up to 75,000 ampullary organs (Wilkens et al. 1997; Wilkens et al. 2001) that allow the fish to detect the passive electric fields of their tiny prey at distances of up to 10 cm and respond by turning appropriately and engulfing the crustaceans in their widespread mouths (Russell et al. 1999; Russell et al. 2001; Wojtenek et al. 2001; Wilkens 2004).

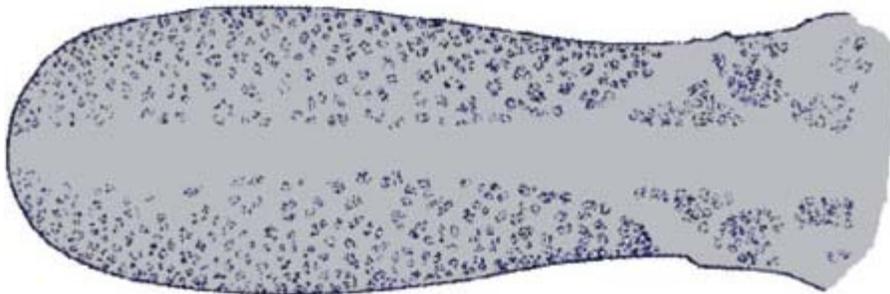


Figure 3. Distribution of ampullary organs on dorsal side of paddlefish rostrum (paddle). Rostrum attaches to remainder of head on right of figure. (After Wilkens 2004.)

Sturgeons (*Acipenseridae*), close relatives of the paddlefish, concentrate their ampullary organs and canals on the ventral side of their heads (Teeter et al. 1980; Gibbs and Northcutt 2004). While both freshwater and marine catfish (*Siluriformes*) distribute ampullary-like receptors over their entire bodies (including the caudal fin), they also have the

greatest concentrations on their heads and especially around their eyes (Peters and Meek 1973; Finger 1986; Northcutt et al. 2000). Interestingly, catfish barbels appear to function only as chemoreceptive and tactile organs and completely lack electroreceptors. The other teleost fish with ampullary-like receptors, the knifefish, elephantfish, featherbacks, and frankfish, all concentrate these organs on the head with a gradient of decreasing density as one moves towards the tail (Zakon 1986; Jørgensen 2005).

A foraging platypus uses a similar array of passive electroreceptors on its bill to detect nearby shrimp, leeches, and other freshwater invertebrates (Scheich et al. 1986; Manger and Pettigrew 1995; Pettigrew et al. 1998; Pettigrew 1999). Both marine and freshwater catfish (*Siluriformes*) combine inputs from ampullary, hydrodynamic, and olfactory organs to detect, track, and capture their prey (Roth 1972; Kalmijn 1974; Finger 1986; Peters et al. 1999; Lorteije et al. 2000; Pohlmann et al. 2004), and North American catfish (*Ictaluridae*) may use their ampullary-like organs to navigate and identify specific locations using local electrochemical fields (Peters and Bretschneider 1972; Kalmijn 1974; Peters and Vanwijla.F 1974; Finger 1986; Kalmijn 1988). Some freshwater catfish may also use passive electroreception to localize and interact with conspecifics in a manner similar to that of marine stingrays (Peters et al. 2002).

In all of these species, the emphasis on passive electroreceptive organs in only one part of the body is surely a result of the limited range over which these stimuli can be detected. Given that most animals are moving in an anterior direction and that passive electroreception is most widely used to detect prey, concentrating the receptors in the anterior end of the animals would seem the logical strategy.

Variations in the frequency tuning of receptors

Another strategy for improving passive electroreception is to tune the maximal responsiveness of the passive electroreceptors to the frequency range of those electric fields that are of greatest interest to the animal. In many cases, the optimal frequencies are those generated by ventilation and locomotion of conspecifics or the animal's prey. In addition to increasing sensitivity to desired stimuli, narrow frequency tuning also excludes irrelevant electrical fields that otherwise would be detected and constitute noise. Although some animals specialize in detecting relatively invariant electrical fields, even these species are most sensitive to stimuli whose amplitudes are at least slightly time-variant. For example, frequencies as low as 0.03–1 Hz will elicit responses in stingrays and catfish, whereas these same animals will ignore a steady field of similar amplitude if neither they nor the source are moving (Finger 1986; Tricas and New 1998; Peters et al. 1999; Tricas and Sisneros 2004). This preference for slightly varying fields is probably due to the fact that there is nearly always some relative motion between the sensing animal and the source of the electrical field. This will transform what the animal perceives from a steady field into a slowly varying one (Hofmann and Wilkens 2005). Because sharks routinely sway their heads left and right as a result of their swimming style, they experience a steady electric field as one that varies in amplitude at a rate of about 1 Hz (Kalmijn 1988). The ampullary receptors of sharks thus require stimuli that vary temporally by at least 1–2 Hz. Rays and skates also favor low frequency stimuli in the range of 0.5–2 Hz (Tricas and Sisneros 2004). Other taxa tend to focus on higher frequencies for passive electroreception: optimal frequency ranges are 2–7 Hz for paddlefish, 6–12 Hz for catfish, 30–50 Hz for knifefish and elephantfish, and 50–100 Hz for the platypus (Zakon 1988; Wilkens 2004; Bodznick and Montgomery 2005).

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