Extended Summary

We are interested in understanding how sharks use electrosensory inputs to locate prey at both the neuronal and algorithmic level. Theses animals are exquisitely sensitive to the dipole-like bioelectric fields of their prey and can rely on these cues in isolation to guide predatory attacks (Kalmijn, 1982). Single organ studies show that the ampullae of Lorenzini provide the brain with information about the intensity and polarity of weak, low-frequency voltage drops that develop across electroreceptor cells in the base of each canal as they move near these sources (Waltman, 1966). Furthermore, information encoded by each primary electrosensory neuron is profoundly affected by the orientation of its innervating canal with the local electric field vector, imparting directional sensitivity to the organ array (Murray, 1974). As a result, the peripheral electrosensory image perceived by the brain is intimately linked to both the spatial structure of the multi-directional array of electro-detectors and the predator's behavioural movements within the field as it hunts.

We have used a quantitative graphical and computational modelling approach to dynamically link the physical geometry and movements of the electrosensory array of a dogfish, *Squalus acanthias* with resulting neural inputs. This allows us to approximate the natural pattern of electrosensory neural inputs in this species as it swims near prey and develop the first neural network model for how these predators electrically-locate prey. The precise three-dimensional physical structure of the ampullae of Lorenzini array was digitally captured using anatomical methods and the resulting graphics imported into the MATLAB computational environment (Berquist & Paulin, 2001) (Fig. 1A). Analytical methods were employed to calculate the electric field distribution

of a prey-simulating dipole in the whole space and compute resulting canal voltage drop development within the electrosensory array as the virtual predator moved nearby (Fig. 1B). Prey was modelled as a localized dipole source with voltage distribution computed using:

$$V(\vec{r}) = \frac{1}{4\pi\varepsilon} \frac{(\vec{P} \cdot \vec{r})}{r^3}$$

where V($\vec{r}$) describes the voltage at distance r from the source in terms of the dipole vector $\vec{P}$. Canal voltage drops were calculated by subtracting the voltage at each pore from that of its ampulla, thus obtaining the instantaneous voltage drop, ΔV, for each canal:

$$\Delta V = V(\vec{r}_{pore}) - V(\vec{r}_{amp})$$

Here $\vec{r}_{pore}$ and $\vec{r}_{amp}$ are the separation vectors between the dipole location and the pore and ampulla, respectively. This completely defines the voltage distribution in the whole space, allowing voltage drops to be computed for each canal. Note that we make the simplifying assumption that the presence of the shark does not distort the distribution of the electric field lines and argue that this does not qualitatively change our results.

To simulate the conversion of canal voltage drop readings into neural spike train information in the virtual dogfish, we approximated the response dynamics of individual primary afferent neurons with a dynamic ranges between 1ηV/cm to 100 μV/cm using a fitted response function, Δf, which captures the characteristics of real neurophysiological data (Tricas & New, 1998): $\Delta f = f - f_0 = \tanh\left(\dfrac{\log(\dfrac{\Delta V}{V_T})}{\log(\dfrac{C_s}{V_T})}\right)$

Here f_0 denotes the rest frequency of the neuron, V_T is the threshold voltage and C_s is a constant that controls the saturation of the frequency input curve. Our model allows for both excitatory and inhibitory voltage drop responses, ranging respectively from >20 to 80 Hz saturation and <20 Hz to 0 Hz. Complete neural occurs with canal inputs around 500 µV/cm with canals experiencing voltage drops higher than this value not contributing significantly more in prey detection decisions than other large-input canals. The behavioural voltage threshold for the model is set at $\Delta V_t = 1$ ηV (Tricas & New, 1998).

Next, we present a neural network hypothesis for how the dogfish may integrate dynamical neural responses to reliably estimate the strength and direction of a prey field. An analysis of the geometric distribution of dogfish ampullary canals reveals sensitivity to electric fields of all directions, with a striking over-representation of electric field directional sensitivity along the axis of forward motion (Figure 2). This strongly suggests that the neural code used by the dogfish to estimate the local electric field is distributed. Our approach therefore is to integrate neural responses from across the entire array, thus making a global decision over the network of neurons. Employing an idea from population coding (Georgeopolis et al., 1986) we show how a small population of 'decision-making' central neurons may be used to process excitatory and inhibitory voltage drop inputs from each electroreceptor. Metaphorically, in the decision-making process each neuron casts a vote that is used to estimate the mean direction and magnitude of the local electric field. To estimate the electric field, the contribution from each canal is defined as:

$$\vec{R}_i = \Delta V_i \cdot \vec{u}_i$$

where $\vec{u}_i$ is the unit vector that runs along the ith canal. Summing these contributions an estimate of the local electric field can be obtained:

$$E_u = \sum_{i=1}^{N} w_i \, | \vec{R}_i | \, (pore_{ui} - amp_{ui}) / length_i, \quad u \in \{x, y, z\}, \quad i \in \{1, 2, ..., N\}$$

where w_i are weighting factors that reflect the relative importance of each canal in obtaining this estimate. Here we assume the simplest case where these weights, w_i, are either +1 or –1, depending on whether a canal is oriented with or against the direction of the electric field. The choice of weighting regime will ultimately depend on what assumptions are made about how the brain processes canal inputs.

To advance the virtual dogfish towards its prey, the electric field estimate is implemented in a behavioral guidance algorithm modeled on orienting behaviors of real sharks approaching dipoles (Kalmijn, 1997). It swims with constant velocity, v = 0.4m/s. Here, the electric field estimate is used, via feedback, to compute the predicted angle that it needs to rotate, in both the horizontal and vertical plane, to orient itself with that electric field direction as it progresses towards the prey. The mouth is used as the center for these movements, and thus prey tracking corresponds to minimizing the distance between the mouth of the predator and its prey. Based on the electrosensory readings, an advance in the direction indicated by the formulae:

$$\begin{cases} l_x = \sum_{i=1}^{N} w_i (pore_{xi} - amp_{xi}) / length_i \\ l_y = \sum_{i=1}^{N} w_i (pore_{yi} - amp_{yi}) / length_i \\ l_z = \sum_{i=1}^{N} w_i (pore_{zi} - amp_{zi}) / length_i \end{cases}$$

The maximum available acceleration that the shark may use for turning is a

monotone function of the magnitude of the integrated responses from the canals. This influences how sharply the shark turns towards the prey and is predicted from the idea that strong electric fields develop in the neighbourhood of the dipole source and thus they require sharp turns. In contrast weak electric fields provide only an approximate estimate of the source that needs to be further refined as the shark gets closer. Furthermore, since noise would affect weak electric field estimates the most, it follows that slow turns are adequate in this situation. This prevents wide turns due to small fluctuations in the medium. The formula used in numerical simulations for maximum available acceleration in the horizontal plane (ie. lateral dogfish movements) is:

$$A_{\max xy} = a_0 \tanh(C_{horizontal} \sqrt{E_x^2 + E_y^2})$$

where a_0 is the maximum centripetal acceleration the shark can achieve. E_x and E_y are the projections of the electric field estimate E on the x and y axis, and $C_{horizontal}$ is a rotational gain constant. Similarly the maximum acceleration in the vertical plane is:

$$A_{\max z} = a_{z0} \tanh(C_{vertical} R_z)$$

As the virtual dogfish attempts to orient with the estimated electric field vector, it re-evaluates its decision at each $t = 0.1$ s interval.

To quantitatively assess the performance of our population coding model for a range of different predator-prey scenarios we use numerical simulations to track virtual approach trajectories in three dimensions (Fig. 4). Here, we consider an example with approaches originating at distances where the electric field is extremely weak. The shark then swims with constant speed towards regions of higher electric field intensity. Successful trajectories result from contact of any part of the mouth with the prey. Two-

dimensional planar trajectories are used to summarize the basic properties of the dogfish electrosensory prey detection process for a systematic range of approach orientations (Fig. 4B), while efficiency sections are used to quantify successful predatory approaches throughout the full three-dimensional space (Fig. 4C).

These methods allow us to generate testable predictions about the neural basis of electric field estimation mechanisms in real dogfish. Furthermore, numerical simulations with virtual canal impairment have been used to explore the functional role of different canal groupings throughout different phases of the prey detection process. In particular, our findings suggest that these fish are most efficient at estimating extremely weak electric fields when their initial approach heading is approximately in line with the direction of the local electric field direction.

In summary, our graphical & computational model of the dogfish electric sense shows how virtual electrosensory inputs approximating the spatial and temporal dynamics of a real dogfish ampullary array can be used by a simple population coding neural network model to reliably estimate the strength and direction of a weak prey electric field. Furthermore, this electric field estimate can be implemented in a simple approach algorithm to reproduce predatory approach trajectories similar to those observed in real sharks locating prey-simulating dipoles.
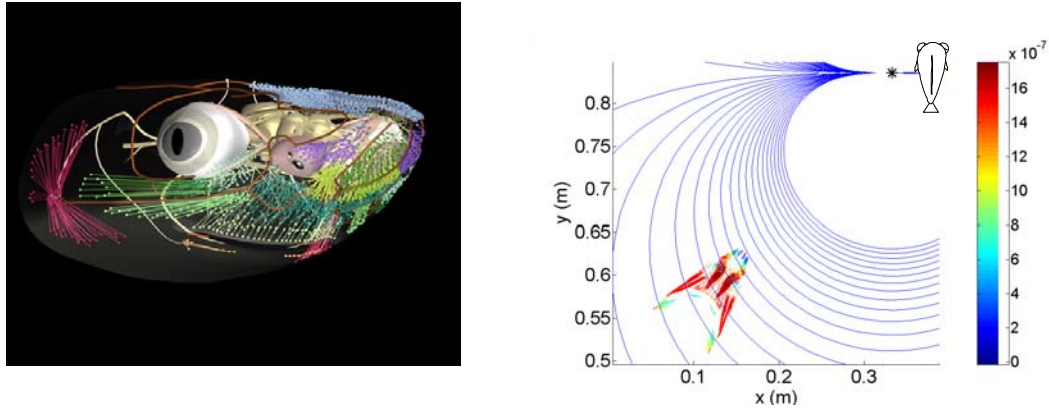
Figures

Fig. 1. (A) The virtual dogfish graphical model. Different canal groups are indicated by colour. (B) 2-D graphic of canal voltage distribution map as the virtual predator moves in a prey electric field. Here, canal colour represents canal voltage drop intensity.
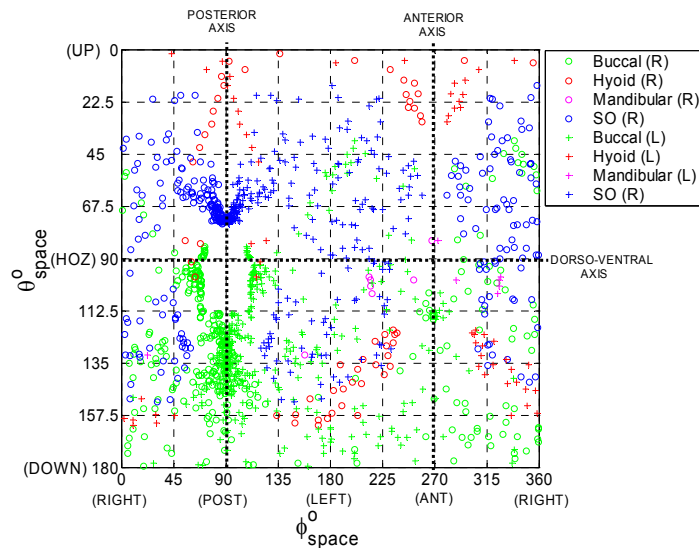

Fig. 2. Spatial orientation of dogfish ampullary canals in spherical coordinates. The angles spanned by each individual canal are represented in polar coordinate phi (φ) & theta (θ) angles.
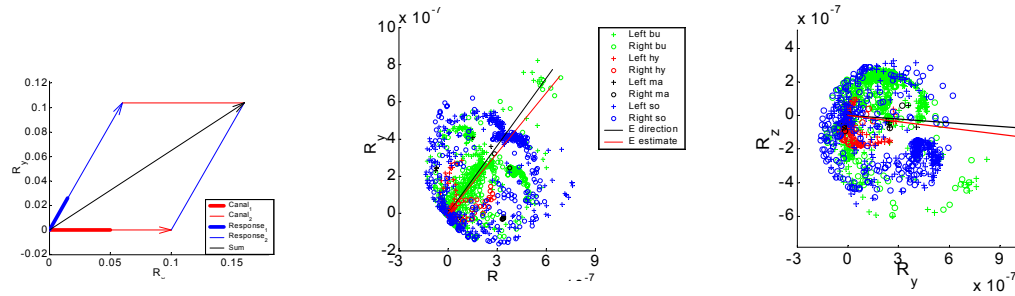
Fig. 3. Computing electric field direction using responses integrated from across the canal array. (A) Responses from two different canals oriented respectively at $\varphi_1 = 60°$ and $\varphi_2 = 0°$ in the horizontal plane ($\theta = 90°$) are summed yielding a response at $\varphi \approx 33°$. (B-C) Summing the individual canal responses (indicated by points in different colours) yields an estimate of the local electric field indicated in red. The actual electric field direction is plotted in black.
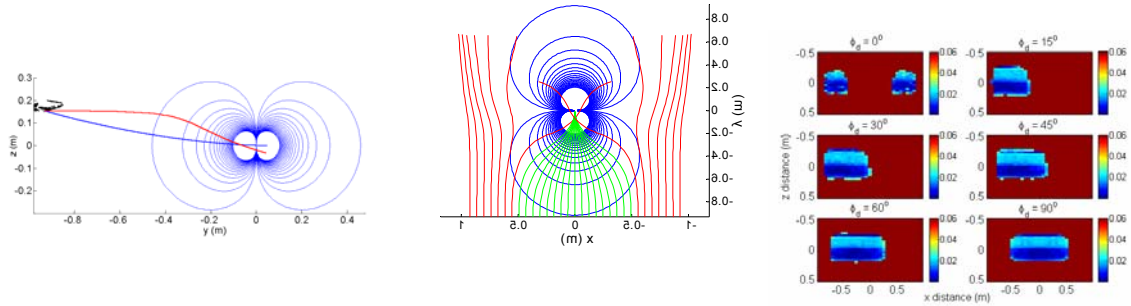

Fig. 4. Examples of prey detection simulation trajectories. (A) Vertical plane view of single trajectories (blue line shows ideal approach trajectory exactly following electric field line contour). (B) 2-D trajectories for multiple predator-prey approach scenarios (green line shows successful prey capture, red shows unsuccessful passes). (C) 2-D efficiency sections. Coloured areas show successful prey capture with colour intensity indicating smallest distance from mouth to dipole origin. Red areas indicate unsuccessful passes.