Article Addendum

Active sensing

Pre-receptor mechanisms and behavior in electric fish

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Weakly electric fish perceive their actively generated electrical field with cutaneous electroreceptors. This active sensory system is used both for orientation and for communication. In a recent paper we focussed on how anatomical adaptations (pre-receptor mechanisms), biophysical constraints and behavior all contribute to active electrolocation, i.e., the fishes’ unique ability to determine and distinguish the electrical properties of objects based on the modulation of a self-generated carrier signal, the so-called electric organ discharge.

How weakly electric fish are able to use the information contained in their own signals has been the centre of many investigations. Several approaches, ranging from psychophysics, modelling and anatomy to neurophysiology, have focused on a key question: what information about an object can fish extract by use of the electrical image? The electric image is the area on the fish’s sensory surface that is influenced by an object under investigation during active electrolocation. The abundance of approaches pursued reflects the difficulty of measuring and quantifying electrical images. Here we extend on our recent results of active electrolocation in Gnathonemus petersii (Günther 1862) and set the stage for a generalisation of problems in electrical imaging.

In essence, information in electrical images is contained in a 2-dimensional distribution of amplitude-modulations of the EOD. Due to a lack of a focussing mechanism (e.g., in vision this would be the lens of the eye), electrical images can be ambiguous. Thus, the shape of an electrical image depends on several object properties and on the distance between the object and the animal (Fig. 1). Additionally, a minimal extend of an electrical image must be projected onto the sensory surface containing the electroreceptor organs (which are embedded in the animals’ skin) in order to extract enough information on object properties. These limitations explain why the electric sense is a near-field sensory system, since far-away objects project incomplete electrical images of reduced amplitude on the sensory surface (see Fig. 1).

Our experiments as well as those of other authors on other electrical fish species have shown that electroreceptor organs occur with highest densities in the peri-oral region, and, in the case of Gnathonemus, especially on the moveable chin appendage, the so-called Schnauzenorgan. In contrast, the density of electroreceptors on the trunk is lower by at least one order of magnitude. These anatomical differences as well as the observation of unique motor patterns and our measurements of the local EOD properties support the hypothesis that there exist two electrosensory foveae in G. petersii: the Schnauzenorgan with its extreme density of electroreceptors and its flexibility is thought to be a fovea used for close-range imaging during foraging; whereas the so-called nasal region (the skin region between the mouth and the nares) might be highly suitable for a detailed analysis of objects in the wider range of active electrolocation.

This idea of two foveae is supported by the body positioning during foraging, when the nasal fovea points forward to perceive approaching, far away objects, while the Schnauzenorgan fovea points downwards and is passed in an oscillating sweeping movement over the ground in order to search for and identify prey items. This focusing of the senses towards the ground has also been found for the eyes of Gnathonemus, where the region of highest ganglion-cell density is also oriented towards the bottom.

While the spatial acuity of electrolocation is expected to be maximal at the foveal regions, the Schnauzenorgan and head are only exposed to a small aspect of an electrical image, especially when the objects are comparatively large, such as those that were used during recent behavioral discrimination experiments. A sensory surface more suitable for the projection of larger electrical images might be the trunk. However, here the spatial acuity is smaller due to the lower electroreceptor density. Physiological data indicate that the trunk, albeit its low receptor density, might be involved in movement/contour-detection.

In addition to the geometrically different shapes of the foveae, the changing properties of the local EOD (lEOD) are another aspect that can lead to ambiguities during active electrolocation. This can be illustrated when the EOD is divided into three vectorial components, representing the three-spatial axis. While the vectorial components of
the EOD are constant and in phase at the head region, they vary at the trunk: the medio-lateral (x-) component increases from head to trunk, while the rostro-caudal (y-) component decreases (Fig. 2A). In addition, the three EOD-components are out of phase at the trunk. This results in a decrease in coherence of the EOD (Fig. 2A). Thus, body shape and local EOD properties result in differences of electrical images at different body regions as is summarised in Figure 2C and D. Hence, in order for the fish to make sense of the information contained in an electrical image, it must take into account which part of the body the image is projected on.

Recent physiological results suggest that the neuronal representation of the trunk sensory surface at the first level of central processing might be optimal for the processing of contours and of movements.8,17 This is in line with modelling data which suggest that the trunk might be the body region suited best for the discrimination between neighbouring objects. Together with our data this strongly suggests that the distribution of the sensory organs and their central representation as well as the constraints for accurate electrical imaging have lead to a functional segregation of different body region, in particular of the two rostral foveae and the trunk.

Our data1 show that in Gnathonemus the electro-sensory fovea at the Schnauzenorgan is unique due to pre-receptor mechanisms which funnel the self-generated current towards its tip. We expect that similar effects are also present in other Mormyrid species, where the highest densities of electroreceptors are also found at the chin.11 Such protuberances are likely to funnel the currents onto the presumed peri-oral fovea.12 Gnathonemus is unique, however, since it actively moves the finger-like Schnauzenorgan in search of food. There are many examples where motion constitutes re-afferent interference during sensory processing,18-22 and electric fish have been most valuable in establishing how corollary discharge information can be used to cancel such interferences.21,22 Our data on the fovea of Gnathonemus adds a yet unprecedented example for a passive suppression of such re-afferent signals. We found that bending of the Schnauzenorgan did not alter the electrical field at its tip.1 Hence the fovea at the Schnauzenorgan can be moved without adding additional ambiguity. This is contrary to swimming movements, which shift the source of the EOD, the electric organ. This leads to modulations of the local EOD at all body regions (Fig. 2B), and these modulations equal those caused by nearby objects. Several studies have shown that corollary discharge mechanisms are employed by the fish to cancel such re-afferent effects. However, convincing examples are still lacking of how the mechanisms proposed10,22 (negative image formation due to synaptic plasticity) can work when the re-afference changes on an EOD-to-EOD timescale.

One general issue emerging from recent models of active sensing3,4 is the contribution of correlations of spatial and temporal aspects to the prevention...
of ambiguities during sensory imaging. Such correlations occur whenever there is relative motion between the fish and an object. In analogy to the visual system,\textsuperscript{23,24} we refer to this as the electrical flow. Recent experiments in \textit{Gymnotus omari}\textsuperscript{25} and \textit{Gnathonemus petersii}\textsuperscript{8,10} have shown that changes in electric images are evaluated with respect to a previous baseline. Thus, changes in electrical flow are detectable and this should enable the animals to perceive spatio-temporal correlations in the electrical flow. The region probably best suited for this is the trunk, where the electroreceptors occur at low density, but their central physiology suggests that this region might be well suited for motion detection.\textsuperscript{17} The foveal regions at the head, in contrast, appear to be more appropriate for accurate detection and discrimination of nearby objects.

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