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Introductory Note

Commentary: Electro-, loco-, and otomotor components of electric fish behaviour

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As beginning neuroscience students, we are taught that behaviour is controlled via output to various types of effectors, with different types of muscles and glands being the prime examples. Later, when we discover the world of weakly electric fish, we learn that the electric organ also qualifies as an effector and that the electric organ discharge (EOD) is a form of motor output. Typically, one of the first behaviours that we then learn about in detail is the jamming avoidance response (JAR; [Bullock et al., 1972](#)). We soon come to appreciate the beauty of the JAR as a behavioural paradigm for studying a complete sensory-motor loop. Because the JAR involves only electromotor output, the full behaviour can be elicited from immobilized animals in the confines of an electrophysiology rig, allowing both neural activity and behavioural output to be monitored simultaneously. Using this powerful approach, Walter Heiligenberg and colleagues were able to functionally map out the neuronal networks controlling the JAR, from sensory input to motor output, at an unprecedented level of detail ([Heiligenberg, 1991](#)). The JAR quickly became one of the most compelling examples of a model system in which behavioural analysis was used to extract both cellular- and systems-level understanding of neurophysiological function ([Konishi, 2006](#)).

The electromotor component of electric fish behaviour tends to stand out because it is something unique that other fish do not possess. It is easy to overlook the more mundane components of fish behaviour, like the locomotor system. Just because locomotor systems are commonplace, however, does not mean we should discount their to provide unique insights into electrosensory function. Indeed, the seminal experiments by [Lissmann and Machin \(1958\)](#) that first demonstrated a clear sensory role for the EOD were based on locomotor, not electromotor, responses of *Gymnarchus*. It is via locomotor output that the fish can approach or avoid a target. Lissmann and Machin made use of locomotor responses in a set of conditioning experiments in which fish were trained to choose between objects of different electrical properties ([Lissmann and Machin, 1958](#)).

In fish, the locomotor system includes muscles that control swimming movements and body posture. In weakly electric fish, the control of body posture has two additional important influences: it determines the position of the electric organ in space and it determines the position and configuration of the electroreceptor array. So, when we speak of the 'locomotor' system of weakly electric fish, this is really shorthand for the motor system

that simultaneously influences the position of the body, the electric organ and the electroreceptor array in 3D space. All three of these aspects are tightly coupled, and it is usually not possible to ascribe a single functional role for any particular locomotor action. In the context of a prey capture task, for example, a body bend may simultaneously move the electroreceptor array closer to the target to enhance sensory signal-to-noise ratio, reposition the electric organ to change the electrical 'illumination' of the target thus providing additional cues for spatial localization, and physically move the mouth of the fish closer to the final target location.

In addition to electromotor and locomotor components, there are what I will call the 'otomotor' components of electric fish behaviour. The prefix 'otro' refers to all the 'other' effector systems that do not directly contribute to EOD modulation or locomotion. This catchall category would include, for example, outputs controlling eye muscles for image stabilisation, jaw muscles for biting, mouth and pharynx movements for prey ingestion and swallowing, and hormonal control of gamete release during spawning. Also included would be the outputs controlling the Schnauzenorgan, a mobile chin appendage of some mormyrids.

Modern behavioural studies of weakly electric fish tap into different aspects of electro-, loco- and otomotor systems to gain insight into electrosensory function. The current issue contains several papers in which these different components of motor output are discussed and analysed, either individually or in conjunction with one another. As an organisational tool, we will group the papers in terms of which motor component is dominant in the behavioural analysis. Electromotor output is featured prominently; four out of the six contributions discussed here have this element front and centre, while two other papers focus more on locomotor and otomotor components.

[Carlson \(this issue\)](#) represents one of the electromotor contributions. The work reported here continues to mine the incredible wealth of the jamming avoidance response as a model system. The focus is on the ambiguity in primary afferent encoding of phase and amplitude modulations in *Eigenmannia*. Traditionally, P- and T-type afferents are thought to encode amplitude and phase modulations, respectively. However, Carlson and colleagues have shown that there is cross coding of these two stimulus features which can give rise to 'phantom' modulations that are not actually present in the stimulus. For example, pure amplitude modulations can be interpreted by the nervous system as a phantom jamming stimulus, giving rise to shifts in the EOD frequency. Even the local amplitude modulation caused by a physical electrolocation target can elicit an EOD frequency shift. These intriguing results demand

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a re-examination of the standard model of primary afferent encoding in this system, and suggest that the EOD frequency in wave species may vary during natural electrolocation tasks.

The paper by [Silva et al. \(this issue\)](#) also deals with modulations of electromotor output. The focus is on seasonal and sexually dimorphic plasticity in the social communication system of *Brachyhypopomus pinnicaudatus*, a pulse-type gymnotid. As a component of reproductive behaviour during the breeding season, males produce EOD accelerations and three different types of chirps, whereas females produce only EOD interruptions. Silva et al. obtained EOD recordings from freely moving male–female pairs both in the wild and in the laboratory. The behavioural results were integrated with anatomical, physiological and pharmacological studies to demonstrate how seasonal and sexual difference could be understood in terms of changes in the sensitivity to glutamate in different areas of the pacemaker nucleus.

[Caputi et al. \(this issue\)](#) reviews principles of active electrolocation in *Gymnotus*, another pulse gymnotid, with an emphasis on electromotor responses to novel electrosensory input. When presented with a sudden increase in local transdermal potential, the fish responds with a transient acceleration of the EOD pulse rate, referred to as a novelty response. Interestingly, a change in local transdermal of the same magnitude in the opposite direction does not elicit this response, so not all ‘novel’ electrical stimuli elicit a novelty response. The magnitude of the novelty response is shown to depend on both the amplitude and the waveform of the ‘novel’ input. The most recent electrosensory image obtained by the fish seems to be compared against an ‘expected’ image that is apparently computed internally based on integration of electrosensory inputs over multiple previous EOD pulses.

The contribution by [Hupé et al. \(this issue\)](#) also deals primarily with electromotor aspects of behaviour, but additionally brings locomotor components into the mix. The paper addresses social interactions in *Apteronotus leptorhynchus*. During agonistic encounters, fish exhibit both electromotor responses (chirping) and locomotor responses (attack lunges). Using correlation analysis, Hupé and colleagues were able to demonstrate that the chirping behaviour of one fish influences both the chirp and attack probabilities of the other fish. The likelihood of a locomotor attack is lower when fish are engaged in electromotor chirping. Thus there is a clear coupling between electromotor and locomotor components of social behaviour.

The paper by [von der Emde et al. \(this issue\)](#) reviews several aspects of active electrolocation in *Gnathonemus petersii*. The behavioural emphasis is on locomotor strategies during electrolocation and ‘otromotor’ aspects involving control of the Schnauzenorgan. When searching for prey, *G. petersii* swims with the body slanted downward and with the tip of the Schnauzenorgan almost touching the substrate. While the locomotor system maintains this body posture and controls forward motion of the fish, ‘otromotor’ outputs are responsible for moving the Schnauzenorgan in a rhythmic, left–right scanning pattern above the substrate. Measurements of the local EOD directly in front of the tip reveal that the electric field moves with the Schnauzenorgan; acting as a sort of electrical searchlight in front of the fish. The paper also reviews the remarkable results of behavioural training experiments showing that the fish can use active electrolocation to discriminate the distance, size, 3D shape, and electrical properties of target objects.

Unlike other studies discussed here, the work by [Landsberger et al. \(this issue\)](#) is aimed at clarifying aspects of behaviour that are mediated by visual rather than electrosensory inputs. In particular, the authors are interested in the visual capabilities of *G. petersii* under dim light conditions. This paper explores an interesting ‘otromotor’ component of visual behaviour in these fish, namely retinomotor activity internal to the eye that leads to structural changes in photoreceptor organization under different lighting

conditions. Using a morphological approach, the authors elucidate the complex ‘grouped retina’ organization of *G. petersii*, in which hundreds of rods and cones are grouped together in bundles. To assess behavioural performance under different lighting conditions, the electromotor response of the fish was recorded as it used its locomotor system to adjust body position relative to a slowly oscillating visual pattern projected onto the ventral visual field. The authors also describe a clever set of training experiments in which *G. petersii* learned to detect a visual pattern displayed on a rear projection screen at the far end of an experimental tank. For the fish to learn this task, it was necessary to first train the fish on an electrolocation task using a 3D metal cube, and then transfer the learned behaviour from the electrosensory to the visual modality.

That brings us to the end of our brief overview of the fascinating behavioural results contained in this issue. What, then, are some of the implications for future studies? In terms of understanding control of electromotor output, there is still a lot to be learned about the contextual dependence of social signalling and the ‘meaning’ of various signals. [Silva et al. \(this issue\)](#) discussed some of the seasonal and sexually dimorphic dependencies, and [Hupé et al. \(this issue\)](#) explored temporal relationships and dependencies between chirp and attack behaviours in interacting pairs of fish. There is still a lot more to be done in this domain. This work will be facilitated by collecting more field recordings of social interactions in the wild (as in [Silva et al., this issue](#)), and by video recordings in the laboratory that allow locomotor components of social interactions to be correlated with electromotor components (as in [Hupé et al., this issue](#)).

For understanding electromotor output in the context of electrolocation behaviours, we need a better general understanding of how EOD output is influenced by variability in sensory input. The EOD frequency of wave species is controlled by what is believed to be the most regular biological oscillator in existence; in fish isolated from sensory modulations, the EOD frequency is extremely precise ([Moortgat et al., 1998](#)). The results reported by [Carlson \(this issue\)](#), showing that pure AMs caused by electrolocation targets can generate EOD frequency shifts, implies that the EOD frequency is probably much less stable than previously thought for fish experiencing dynamic AMs in real world situations. It would be worthwhile to characterize the degree of EOD frequency variation observed for individual wave-type electric fish exploring naturalistic environments. Then one could explore the impact of this variation, if any, on electrolocation performance.

The fact that pure AMs can bring about EOD frequency shifts in wave species calls for a re-examination of so-called ‘novelty’ responses across both wave and pulse species. Are the EOD accelerations observed in pulse gymnotids ([Caputi et al., this issue](#)) more similar to the phantom ‘JAR-like’ EOD frequency change observed in wave gymnotids ([Carlson, this issue](#)) or the ‘novelty’ responses of pulse mormyrids ([von der Emde, this issue](#))? This question needs to be addressed both in terms of neural substrates and in terms of functional consequences.

On the locomotor front, it is clear that body posture and position play an important role both in social interactions and in electrolocation tasks. As mentioned earlier, it is not just the position of the body *per se*, but the position and orientation of the electric organ and the configuration of the electroreceptor array that influence these tasks. In the future, we can expect to learn a lot from detailed video analyses of locomotor strategies used during social interactions and electrolocation behaviours. For example, in the object discrimination experiments described by [Landsberger et al. \(this issue\)](#) in which *G. petersii* first learns an electrosensory-based task and later transfers this to a visual task, it would be interesting to know whether the sensory acquisition strategies of the fish change depending on the modality being used to make the discrimination. Does the fish control body position, posture, and EOD pulse rate differently for visual versus electrosensory discrimination?

In terms of 'otromotor' outputs, control of the Schnauzenorgan is clearly a rich area for further investigation. Also, the control of mouth opening and closing may be of interest in some species. The low impedance pathway afforded by an open mouth serves to 'funnel' electric current in the forward direction. In *G. petersii*, the mouth appears to be constantly open, but what happens in species that can voluntarily open and close the mouth? Are there any cases in which the fish make use of this ability to modulate the electric field pattern, either in the context of electrolocation or social signalling? When a fish gapes its mouth open in the direction of another fish, what are the electrosensory consequences as perceived by the other fish? In fish lacking a Schnauzenorgan, can the mouth be used to modulate the local electric field immediately in front of the fish when scanning the substrate for prey?

Finally, the study by Landsberger et al. (this issue) on dim light vision in *G. petersii* should remind us to not overlook other sensory modalities. In addition to the active electric sense, weakly electric fish are constantly collecting sensory information from the passive electric sense, the lateral line mechanosense, vision, olfaction and touch. Not only is this a reminder that we should include appropriate controls when using behavioural approaches to assay active electrosensory performance, but it opens up a range of interesting possibilities for studying behavioural aspects of multimodal sensory integration in these animals.

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