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The decoding of electrosensory systems

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Progress in the study of electrosensory systems has been facilitated by the systematic use of behavior as a tool to probe the nervous system. Indeed, a specific behavior that is found in a subset of weakly electric fishes, the jamming avoidance response, was used to identify and characterize an entire suite of brain circuits, from sensory receptors to motor units, that are involved in control of this behavior. Recent progress has focused on a re-analysis of this circuit in relation to newly described electrosensory behaviors, including prey capture, social signaling and the tracking of electrosensory objects. This re-analysis has led to a re-evaluation of the broader functional relevance of specific neural solutions to computational problems that are related to the control of the jamming avoidance response. Some of the recent insights that have emerged from this work include descriptions of mechanisms underlying dynamic receptive field properties, descriptions of the neural activity related to simultaneously occurring sensory stimuli, and a greater understanding of the role of short-term synaptic plasticity in temporal processing.

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Current Opinion in Neurobiology 2006, 16:1–7

This review comes from a themed issue on
Sensory systems
Edited by Yang Dan and Richard D Mooney

0959-4388/\$ – see front matter
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DOI 10.1016/j.conb.2006.06.006

Introduction

A central goal of neuroscience is to describe how neural circuits represent sensory information and control behavior. A first step towards this goal is to generate a description of sensory and motor parameters of experimentally tractable behaviors. This description can be used to probe the brain to identify and characterize spatiotemporal patterns of spiking that are associated with particular behavioral functions. These correlations between brain activity and behavior are the basis for functional and mechanistic analyses of neural networks. Finally, insights from this work can be used as a tool to identify new aspects of the original behavior or totally new behaviors for further analysis of the system.

Some of the greatest progress in decoding brain mechanisms for behavior has been achieved in the study of the electrosensory systems in weakly electric fishes. This achievement was based, in part, on the description of a complete sensory algorithm for the control of a robust electrosensory behavior known as the jamming avoidance response (JAR) that occurs in several species of weakly electric fishes. During this behavior, an individual fish responds to specific, detrimental electrosensory conditions that occur in social situations by changing aspects of its electric field. The JAR behavior remains intact during electrophysiological studies, and has been used to reveal the central nervous system (CNS) codes and functional computations in the entire neural circuit, from the level of the receptors through each stage of processing in the CNS ending with the motor units [1,2]. This well understood neural circuit is now being reassessed in relation to recently characterized features of the JAR and other electrosensory behaviors.

This review focuses on recent work that illustrates how this re-analysis of the JAR circuitry in the context of these electrosensory behaviors is generating exciting new insights into fundamental mechanisms for neural processing in sensory systems. The foundations for this work are behavioral analyses, including features of the JAR, social signaling, prey capture and electrosensory tracking behavior. These behaviors roughly define two categories of salient electrosensory stimuli: global stimuli and local stimuli. Global stimuli synchronously activate wide swaths of the sensorium, whereas local stimuli activate small patches of the sensory sheet. The analysis of these behaviors has led to new neural insights of general interest: these include dynamic features of receptive field properties that depend on the spatial aspects of electrosensory stimuli, the simultaneous processing of two or more salient stimuli, and the role of short-term synaptic plasticity and gamma band oscillations in temporal and spatiotemporal processing.

After a brief overview of some basic features of electrosensory systems, the behaviors that are the basis for the re-analysis of the CNS circuits that were previously studied in relation to the JAR are discussed. The behaviors are divided into two categories — those that involve global stimuli and those that involve local stimuli. The review concludes with a description of the insights into neural processing that have resulted from these behavioral observations.

Electrosensory systems

Electroreceptors have been found in a wide array of aquatic vertebrates, including sharks, rays, bony fishes,

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amphibians, and in the monotreme *Platypus* [2,3]. The electrical signals detected by electroreceptors originate from a number of sources, including the geomagnetic field, objects in the environment, biological materials and activity, and certain electrogenic organisms [1–5]. Electroreceptors are, in a way, similar to extruded visual systems — the energy fluxes that are transduced by these systems travel at the speed of light, and there is a direct correlation between object size and distance and the pattern of activation on the sensorium [6]. Similar to the case with visual systems, aquatic animals use electroreceptors to perceive spatially complex, time-varying signals such as prey and objects in the environment [6,7,8,9,10].

The most common electroreceptors are ampullary receptors; this class of receptors is ancient, phylogenetically widespread, and encodes naturally occurring low-frequency signals, typically below 100 Hz [2,3]. An additional electroreceptor modality is found in electrogenic species, including South American Gymnotiform fishes and African Mormyrid fishes, which is tuned to the features of the electric field produced by their own species. This modality is mediated by a variety of types of tuberous electroreceptors — individual species commonly have more than one type of tuberous electroreceptor. Weakly electric fish use the self-generated electroreceptor signals to identify and characterize objects in the environment [6], in prey capture [9,10], and in social communication [11]. Weakly electric fishes, therefore, have at least two parallel electroreceptor systems: the ampullary system that detects signals that typically originate from external sources and the tuberous systems that detect signals resulting from the electric field generated by the fish.

If we were to think of these electroreceptor systems in terms of the human visual system, it would be similar to humans having two photoreceptive systems and a special light-emitting organ. The first photoreceptive system would be our normal eyes, which detect ambient light (similar to the ampullary system), and the second system, a new specialized visual system, would only detect the light emitted by the light-emitting organ (similar to the tuberous system). In this way we could see in the absence of externally generated visual signals — we could see at night using the combination of the light-emitting organ and the specialized photoreceptors. Indeed, sensory perception at night is one of the functions of electrogenesis in these nocturnal fishes. These self-generated sensory signals present an interesting new problem — what happens when the signals of nearby animals interact? In weakly electric fishes, the interaction of the fields generated by nearby conspecifics will result in predictable interference patterns. Depending on the species, some patterns of interference can lead to a dramatic degradation of electroreceptor function, which is known as ‘jamming’.

Electrosensory behaviors

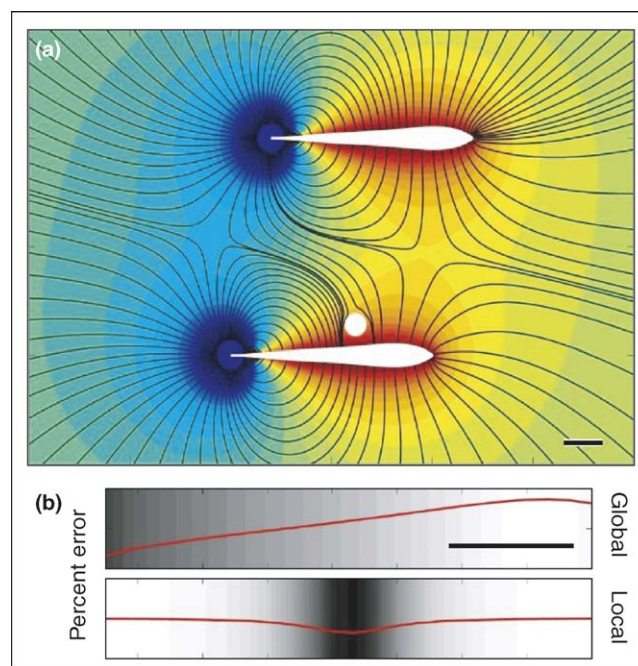
Some electroreceptor behaviors, including the JAR, involve global electroreceptor stimuli, whereas other behaviors involve local stimuli. Global electroreceptor stimuli are those that activate many or all of the electroreceptors at the same time. Thinking of the human visual system, a global stimulus might include the raising and lowering of ambient light levels, such as might happen when turning a light dimmer up and down. A strobe light could also be a form of global stimulus. By contrast, local stimuli activate small regions of electroreceptors. A local stimulus in the visual modality might be the movement of a small light or object within the visual field. Global and local stimuli can, importantly, occur simultaneously.

Global electroreceptor stimuli

The jamming avoidance response

When weakly electric fish are in close proximity, their electric fields mix. The electric fields from each fish will stimulate electroreceptors on each of the other nearby fish. This stimulation is global in that it will include most, if not all, electroreceptors on the body surface of each animal (Figure 1). In short, there is a

Figure 1



Model of the electric fields of *Eigenmannia* [8,26,27]. (a) A view from above of the electric fields of two electrogenic fishes and a small insulating object. Color gradients indicate voltages and black lines indicate the electric field lines. (b) The voltage difference between the perturbed and the unperturbed fields, measured along the skin, resulting from the interaction between the electric fields of the two fishes (global) and from the object (local). The local signal produces a pronounced signal in a spatially restricted region of the skin, whereas the global signal produces a graded signal across the entire receptor sheet. Scale bars indicate 2 cm. Figure credit: Eatai Roth.

categorical difference between fish that are alone and those that are in groups of conspecifics: fish in groups experience ongoing, global electrosensory interference patterns, whereas solitary fish do not.

Weakly electric fish employ a variety of behavioral and computational solutions to avoid the potentially detrimental interference patterns that result from the mixing of the electric fields of nearby conspecifics. The solution that has been studied in the greatest detail is the JAR of the glass knife fish, *Eigenmannia virescens*. *Eigenmannia* produce continuous, nearly sinusoidal electric fields in the range of about 200 to 700 Hz. When two fish of similar electric organ discharge (EOD) frequencies are within about 1 meter of each other, the combination of their EODs produces global amplitude and phase modulations that can interfere with the ability of both animals to electrolocate [12]. Modulation rates (also known as beat rates) of between 3 and 8 Hz are most detrimental to electrolocation, and elicit the largest JARs, whereas beat rates of 20 Hz do not impair electrolocation [13–16]. During a JAR the fish with the lower initial EOD frequency lowers its frequency while the other fish raises its frequency, thereby increasing the beat rate to values that have little known effects on electrolocation. The JAR, therefore, ensures that these fish will only briefly, in the order of seconds, experience detrimental beat rates of 10 Hz or less. *Apteronotus* exhibit a similar behavior, except that in this species the JAR involves only increases in EOD frequencies [13].

A consequence of the JAR and gregarious social behavior [17^{••}], as observed in the natural habitat and in the laboratory, is that most *Eigenmannia* routinely experience ongoing beat rates of 20 to 80 Hz [18[•]]. These ‘post-JAR’ global electrosensory oscillations, which continue for as long as fish remain in close proximity, result in the global activation of electrosensory brain circuits at the same rates. The post-JAR patterns of activation are not unlike those described as ‘gamma band oscillations’ in many other systems [19,20]. In general, gamma band oscillations are patterns of synchronous activity in large arrays of neurons at rates of around 40 Hz (reports range from 20 to 80 Hz). The situation is similar in other closely related genera including *Apteronotus*: an outcome of the JAR is that fish experience ongoing sensory-driven post-JAR gamma band oscillations when in groups but not when alone.

Social signals

Communication signals in weakly electric fish include modulations of the autogenous electric field: the structure of these signals varies among species [21,22]. A common feature of communication signals is that they result in global activation of electroreceptors in the receiver. The communication signals of *Apteronotus* have received the most attention, and among the communication signals that these fish produce, chirps are both the most common and

the best understood [11]. Chirps are frequency and amplitude modulations of the ongoing electric field with durations that are in the order of 10 s to 100 s of milliseconds. The most commonly produced chirps in *Apteronotus* are short amplitude modulations with durations of around 20 ms (50 Hz) [23]. Other signals include gradual frequency rises, and at least four other types of chirps [24,25].

Local electrosensory signals

Natural objects in the water, such as plants, prey, and other animals, produce more localized electrosensory images. Unlike visual stimuli, however, the dynamic structure of salient electric fields around weakly electric fish is not well understood. Recent studies have nevertheless made significant progress in the measurement and modeling of these electric fields (Figure 1) [8[•],26–28]. Furthermore, behavioral phenomena have been used to identify new categories of salient, local electrosensory stimuli. In general, these signals result in more localized activation on the sensorium than the signals that are used in the control of the JAR.

Prey capture

One of the most interesting behavioral studies of electrosensory processing has been the detailed characterization of prey capture in *Apteronotus* [9,29–31]. High-speed videos were made of unrestrained prey capture (the prey were *Daphnia*). These were digitally encoded, and models of the body position and electric field of the animal were fitted throughout the behavioral sequence. In short, *Apteronotus* use longitudinal and bending motions to draw the prey item along the body towards the head where the highest density of electroreceptors is found. Once the item is near the head, the fish reverses direction and strikes the item. Careful analyses and mathematical models of this behavior provided detailed estimates of the electric field perturbations that were produced by the prey items and the motion of the fish [30].

Considering the relative movement of the fish and prey, the size of the receptive fields, and the oscillatory movements of the prey, the models reveal that most salient information during prey capture occurs at rates of 10 Hz or below. These local stimulation frequencies, interestingly, overlap with the frequencies of global stimuli (beat rates) that maximally impair electroreception and trigger the JAR. In addition, these frequencies are well below those frequencies of post-JAR global stimuli. Similar analyses have also been achieved for ampullary processing in paddlefish [10], which are not electrogenic and do not exhibit the JAR behavior. Electrosensory signals from plankton and from *Daphnia* stimulate paddlefish electroreceptors at similar rates, up to approximately 15 Hz.

Tracking behavior

Another behavioral analysis of electrosensory processing takes advantage of the fact that *Eigenmannia* and other

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species of weakly electric fish maintain their position in tubes or near objects or hiding places. These animals will actively maintain their relative position to the surrounding objects, even when the objects are moved [7,12,32–34]. Experiments that measure the longitudinal motions of the fish in response to experimenter-controlled movement of an object or refuge enable an assessment of the sensory and motor systems of the animal. These tracking behaviors have fewer degrees of freedom than prey capture, but offer greater experimental control and can rely on the tight stimulus–response relationships for analysis. Fish will track the motion of these large objects at oscillation rates at least up to 0.5 Hz at speeds of greater than 5 cm per second [34,35]. Objects with similar sizes elicit responses in midbrain neurons at rates from 2 to 15 Hz [36•]. Again, these rates are similar to those that, for global stimuli, both impair electrolocation and trigger the JAR.

Processing of global and local electrosensory signals in central nervous system circuits

The behavioral analyses described above have revealed new insights concerning behaviorally relevant electrosensory signals. Local electrosensory signals, which include moving and/or oscillating objects, result in stimulation rates that are commonly less than 10 Hz. By contrast, global signals that result from the fields of nearby conspecifics, which include post-JAR oscillations and communication signals, typically result in stimulation rates of 20 Hz or more. Importantly, salient local stimuli and global stimuli, particularly the post-JAR signals, can occur simultaneously.

Dynamic receptive field properties

Global and local signals elicit different encoding features at the first CNS stage of processing, the electrosensory lateral line lobe (ELL). The responses of ELL neurons are crucially dependent on the spatial extent of electrosensory stimuli [37,38•,39,40,41••]. Of particular interest in this regard is a switch in temporal processing: under global stimulation, pyramidal neurons in the ELL best encode higher frequency stimuli of 20 Hz or more, whereas under local stimulation, the same pyramidal neurons best encode lower frequency stimuli of less than 20 Hz [39]. Because global stimuli, including ongoing post-JAR oscillations and many social signals, occur at higher frequencies (~20 Hz and above), and local stimuli, particularly prey and objects in the environment, occur at lower frequencies (~10 Hz and below), these pyramidal neurons appear to be dynamically matching the information processing characteristics to the expected information content from different sources.

What are the mechanisms for this switch in information processing? Inactivation of descending feedback dramatically reduces the differences in response properties to global and local stimuli [39,41••]. Changes in the response

to global stimuli underlie this change — the suppression of low-frequency responses appears to be removed when the feedback pathway is interrupted. Heterogeneities in the populations of pyramidal cells offer additional clues: superficial pyramidal cells exhibit the greatest changes, whereas deep pyramidal cells exhibit little or no changes. The superficial cells have the largest apical dendrites and were found to have the greatest change from local to global stimulation in nonlinear encoding models, whereas deep pyramidal cells showed no significant change [41••]. Superficial cells have larger receptive fields (prefer more global stimuli) and, importantly, receive more descending feedback [37,38•].

Detection of communication signals

Electric communication signals require the simultaneous processing of two global stimuli: post-JAR oscillations and the communication signal itself. In *Apteronotus*, spike frequency adaptation, a form of habituation, enables animals to separate ongoing oscillations from salient chirp signals [42•]. Spike frequency adaptation is common in receptor afferents of a variety of modalities and species, and could be a general mechanism for the enhanced encoding of transient salient stimuli. Another mechanism that appears to enhance the detection of chirps has been observed in the electrosensory midbrain. In *Eigenmannia*, a subset of neurons in the electrosensory midbrain have QX-314 (a pharmacological agent) sensitive Na⁺ conductances [43]. These conductances, which are independent of the spike generating Na⁺ conductances in these neurons, produce all-or-none post-synaptic potentials (PSPs) that have durations that are similar to chirp stimuli. This matching of PSP durations and the underlying sensory stimulus can enhance the responses to chirps by more than four times [43].

Simultaneous processing of global and local stimuli

Information from the ELL is passed to neurons in the torus semicircularis (midbrain). Local stimuli, such as a moving bar, can elicit strong responses from midbrain neurons. Simultaneous presentation of moving local stimuli and global stimuli, however, demonstrates an interaction between local and global information [36•]. Presentation of a moving stimulus in the presence of detrimental global stimuli of 10 Hz or below results in a dramatic attenuation of responses to the moving stimulus. This interaction suggests that the feedback pathways in the ELL not only shift the temporal processing features of pyramidal neurons but also gate the flow of local information [36•]. The mechanism for this gating is not currently known, but could be related to the production of bursts for low frequency stimuli [44•,45••].

By contrast, the presentation of moving stimuli simultaneously with post-JAR global stimuli of 20 to 50 Hz elicits combined responses that represent both the global and the local (moving object) stimulation frequencies [36•].

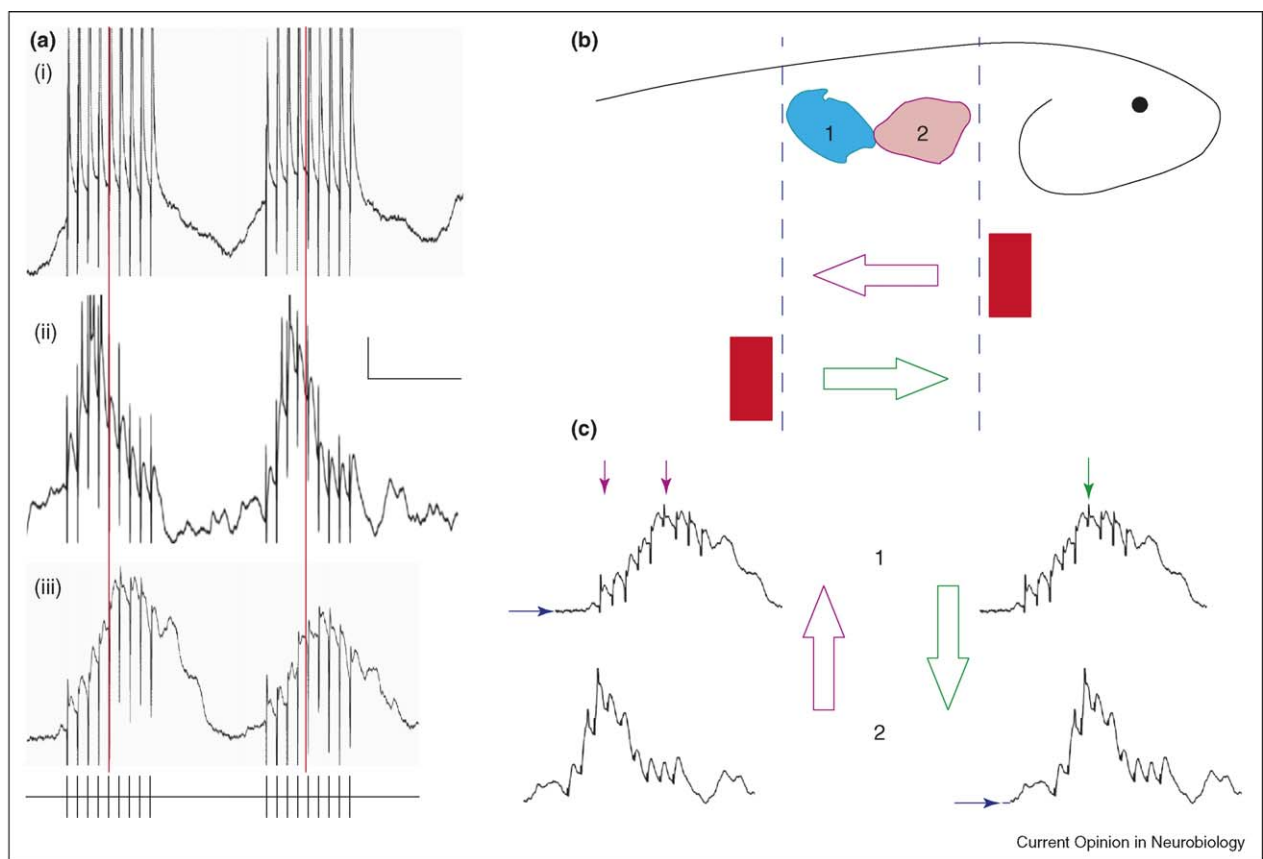
The responses to the moving object with the concomitant post-JAR signals differ, however, from responses without the post-JAR signals. In the presence of the post-JAR global signals, neurons exhibit a greater difference in the responses to head-to-tail versus tail-to-head motion of electrosensory objects [46^{*}]. This increase in directionality is achieved by the attenuation of an excitatory post-synaptic potential (EPSP) in response to one direction of movement of electrosensory objects.

Strong correlations between the magnitudes of direction selectivity and a measure of short-term depression to global stimuli suggest that short-term plasticity could be a mechanism for the generation of direction selectivity in these neurons [46^{*}]. One consequence of short-term synaptic plasticity in the midbrain includes relative phase shifts — depression leads to phase advances,

whereas facilitation leads to phase delays (Figure 2) [47,48]. Theoretically, these plasticity-based phase advances and delays could be used to generate directional responses [49]. According to this hypothesis, information from adjacent receptive fields would be combined through synapses with different plasticity-based delays. As a result, movement of an object in the preferred direction would lead to simultaneously occurring peak responses and movement in the opposite direction would result in peaks occurring at different times (Figure 2).

It is possible, therefore, that the enhancement of direction selectivity by the addition of the global post-JAR signals might result from the effects of the global signals on short-term synaptic depression. In this model, the global, post-JAR signals altered the timing and magnitude

Figure 2



Relationships of short-term synaptic plasticity and spatiotemporal processing [48]. **(a)** Intracellularly recorded responses of three midbrain neurons to identical trains of afferent stimulation with bipolar electrodes (lateral lemniscus). Stimulation trains were composed of nine pulses with 10 ms interpulse intervals. **(i)** Neuron that did not exhibit short-term synaptic plasticity. **(ii and iii)** The responses in neurons with short-term synaptic depression and facilitation, respectively. **(ii)** The middle neuron is phase-advanced, and **(iii)** the bottom one phase-delayed when compared with the neuron **(i)** without short-term synaptic plasticity. **(b)** A moving stimulus passing through two receptive fields. Top purple arrow is movement of the object from head to tail, and bottom green arrow is from tail to head. **(c)** In this example, PSPs from receptive field 1 show short-term facilitation, and those from field 2 show depression. In the head to tail direction of motion (open purple arrows) the peaks of the responses in the two neurons occur at different times (small purple arrows). By contrast, tail to head direction of object motion (open green arrows) elicits peak responses from both neurons at the same time (small green arrow). In this way short-term synaptic depression can function as a form of delay line for temporal processing [49].

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of the plasticity-based delay lines to the moving object. This change in the timing and magnitude of short-term synaptic plasticity led to an enhancement of direction selectivity in response to the moving object. If this model is correct, the global synchronous gamma band oscillations that occur in many neural circuits could be a general mechanism that is used to modulate short-term synaptic plasticity for the purpose of enhancing temporal and/or spatiotemporal processing of more local streams of information.

Conclusions

Our understanding of how neural circuits represent and control behavior depends on the observation of correlations between behaviourally relevant signals and brain activity. There has been a renaissance in the study of electrosensory systems as new analyses of electrosensory behaviors, including the JAR, prey capture, social communication, and tracking, have led to a greater understanding of behaviourally relevant electrosensory stimuli. As a result, dramatic new correlations between brain activity and behavior have been identified. Of particular interest are the mechanisms that have been identified for the generation of dynamic receptive fields, simultaneous processing of more than one sensory stimulus, and the possible role of global synchronous gamma-band activity in the modulation of single-neuron temporal processing through short-term synaptic plasticity.

Acknowledgements

E Roth produced the model and plot in Figure 1. N Cowan and G Ball helped with reviews of the manuscript. R Mooney provided both crucial insights and suggestions that significantly improved the manuscript.

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