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REVIEW

The processing of proprioceptive signals in distributed networks: insights from insect motor control

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ABSTRACT

The integration of sensory information is required to maintain body posture and to generate robust yet flexible locomotion through unpredictable environments. To anticipate required adaptations in limb posture and enable compensation of sudden perturbations, an animal's nervous system assembles external (exteroception) and internal (proprioception) cues. Coherent neuronal representations of the proprioceptive context of the body and the appendages arise from the concerted action of multiple sense organs monitoring body kinetics and kinematics. This multimodal proprioceptive information, together with exteroceptive signals and brain-derived descending motor commands, converges onto premotor networks – i.e. the local neuronal circuitry controlling motor output and movements – within the ventral nerve cord (VNC), the insect equivalent of the vertebrate spinal cord. This Review summarizes existing knowledge and recent advances in understanding how local premotor networks in the VNC use convergent information to generate contextually appropriate activity, focusing on the example of posture control. We compare the role and advantages of distributed sensory processing over dedicated neuronal pathways, and the challenges of multimodal integration in distributed networks. We discuss how the gain of distributed networks may be tuned to enable the behavioral repertoire of these systems, and argue that insect premotor networks might compensate for their limited neuronal population size by, in comparison to vertebrate networks, relying more heavily on the specificity of their connections. At a time in which connectomics and physiological recording techniques enable anatomical and functional circuit dissection at an unprecedented resolution, insect motor systems offer unique opportunities to identify the mechanisms underlying multimodal integration for flexible motor control.

KEY WORDS: Multimodal integration, Proprioception, Distributed processing, Dedicated pathways, Sensorimotor networks, Locomotion

Introduction

To ensure the survival of an animal in varying, unpredictable environments, its nervous system processes and integrates a multitude of sensory and internally generated neural signals (Fig. 1A). Neural networks monitor the body's current internal and external state to generate a context-dependent representation and, subsequently, appropriate and adaptive behavioral responses. For example, visual information about a moving object is combined with coinciding chemosensory information to distinguish conspecific males from females and to decide between aggressive or courtship behavior in fruit flies (Pavlou and Goodwin, 2013). Multimodal perception requires precise and coordinated temporal and spatial processing of incoming sensory signals, the details of which are the subject of an ongoing debate in the neurosciences (Arber and Costa, 2022; Dokka et al., 2015; Fisher, 2022; Fujiwara et al., 2022; Metaxakis et al., 2018; Ng et al., 2020; Roth et al., 2016). Motor systems promise to provide insights into these mechanisms, as they rely on the integration of diverse sensory inputs and provide experimentally measurable outputs. These sensory signals are used to maintain stable, coordinated body posture – both at rest, against gravitational forces and external perturbations, and during active movements, such as locomotion, to coordinate body wall muscles and fin muscles in swimming, leg muscles in walking and wing muscles in flight. Except for exceptionally fast movements, e.g. giant neuron-mediated escape responses (fruit fly: Allen et al., 2006; cockroach: Comer et al., 1988; goldfish: Faber et al., 1989; crayfish: Wine and Krasne, 1972), motoneuronal activity and the resulting movements rely on online (i.e. ongoing and continuous) processing and integration of sensory feedback from the body and its appendages (for reviews, see Hooper and Büschges, 2017; Orlovsky et al., 1999). Specific relevance is attributed to proprioceptive feedback, i.e. sensory information about movements and forces arising from the animal's own motor activity (Fig. 1A; Edwards and Prilutsky, 2017). Across vertebrate and insect species, neural pathways contributing to proprioceptive integration have been identified (Agrawal et al., 2020; Chen et al., 2021; Gebehart et al., 2021; Picton et al., 2021; Santuz et al., 2022; Tuthill and Wilson, 2016a; for prior work, see Bässler, 1993; Burrows, 1996; Schomburg, 1990). The identified pathways display a network architecture that has been termed 'distributed' processing; distributed networks (see Glossary) appear to play a major role in sensorimotor integration and the subsequent generation of motor output and control of posture and movements.

The current state of knowledge on proprioception, its general concepts, function in locomotion and posture control, and its sensory origins, both in vertebrates and insects, have been summarized in previous reviews (Bosco and Poppele, 2001; Grillner and El Manira, 2020; Pearson, 1995; Tuthill and Azim, 2018; Windhorst, 2007). In this Review, we aim to provide an overview and a perspective on the architecture of networks underlying proprioceptive processing and integration, with a specific focus on insects. Insects provide a unique opportunity to study network architecture in a nervous system with limited numbers of neurons, thus drastically reducing the number of circuit elements of that need to be studied and controlled. Additionally, these animals are readily amenable to mechanical and – especially in the case of *Drosophila melanogaster* – genetic manipulations, thereby allowing sensorimotor circuits and function to be more easily investigated. To date, insects have provided important insights relating to proprioception and distributed processing; here, we aim to

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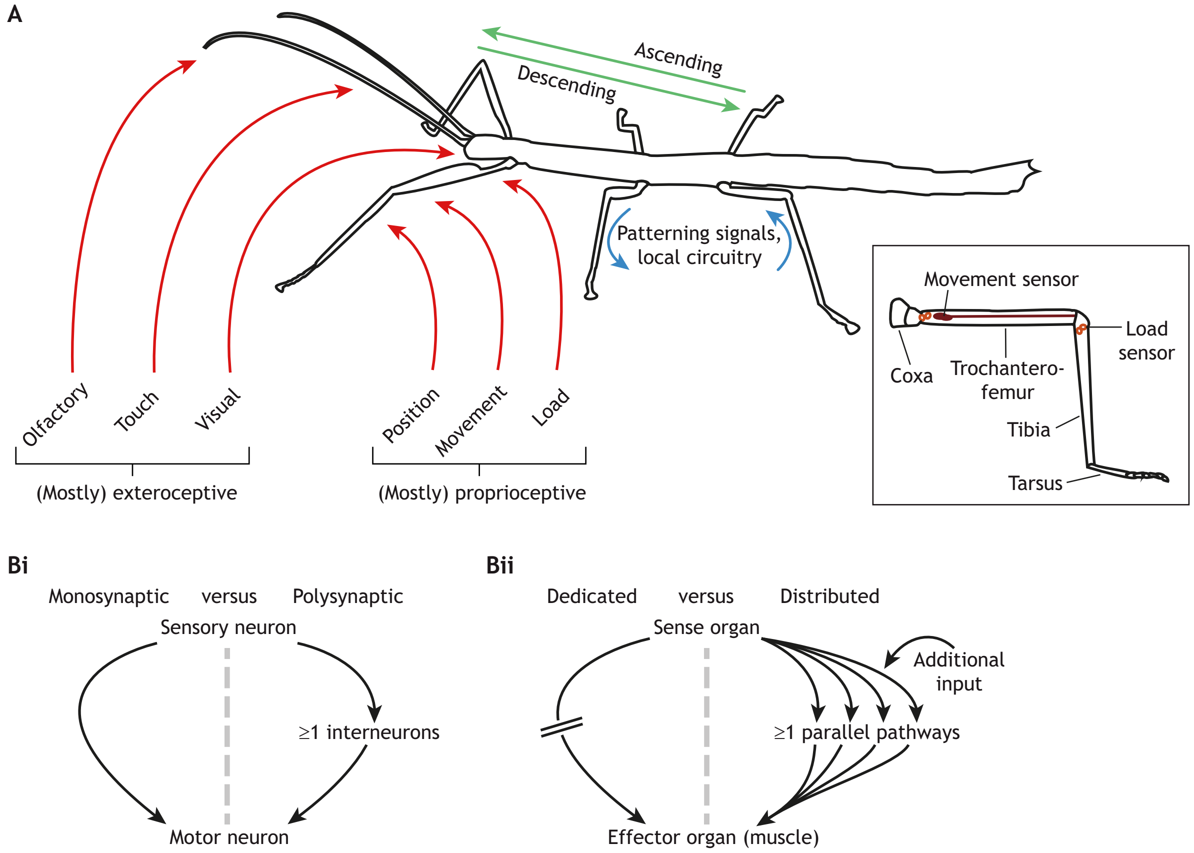

Fig. 1. Schematic representation of the types of signaling pathways involved in motor control. (A) Examples of exteroceptive and proprioceptive feedback (red) that the nervous system integrates with internally generated patterning signals in local circuits (blue), and transmits from the brain to the ventral nerve chord (VNC), or from the VNC to the brain, via descending and ascending pathways, respectively (green). Note that the distinction between exteroceptive and proprioceptive feedback cannot always be drawn clearly and can depend on the behavioral context of the animal, e.g. sensors monitoring leg joint position signal both self- and externally generated leg movements. Inset: insect leg segments and examples of proprioceptive sense organs. (Bi) Schematic representation of monosynaptic versus polysynaptic signaling pathways. In polysynaptic signaling, one or more interneurons are intercalated between the sensory and motor neurons. The depicted circuit motifs can be localized to single neuromeres or, in the case of polysynaptic pathways, can span across segments. (Bii) Schematic representation of dedicated versus distributed signaling pathways. In dedicated processing, the signal is transmitted along a single pathway from sense to effector organ. Interrupted arrow indicates that dedicated pathways do not necessarily have to be monosynaptic. In distributed processing, the information is transmitted, shaped and potentially integrated with additional inputs by multiple pathways acting in parallel. Note that both dedicated and distributed processing can be polysynaptic.

highlight these contributions. We first introduce the current state of knowledge on the network topology (see Glossary) of unimodal (see Glossary) proprioceptive feedback processing for posture control. We then broaden this view to a multimodal (see Glossary) sensory perspective, discussing the advantages and challenges of relying on distributed processing for building efficient control architectures for motor systems, and the functional insights into how network gain (see Glossary) is modified in distributed neuronal circuits controlling motor output and movements, i.e. distributed premotor networks (see Glossary). We will touch upon the importance of lateral connectivity (see Glossary) within these networks and, finally, consider potential directions for future investigation of the neural mechanisms underlying flexible and task-specific motor control of animal movements in general.

Dedicated versus distributed processing of proprioceptive feedback in a locomotor system

In vertebrates and invertebrates, posture control is mediated by proprioceptive signals tuning the activity of motor neurons both through direct, monosynaptic connections from sensory to motor neurons (e.g. locust: Burrows, 1987; crayfish: El Manira et al., 1991; vertebrates: Jankowska, 2013b; Matthews, 1972; cockroach: Pearson et al., 1976; *Drosophila*: Phelps et al., 2021) and through parallel polysynaptic pathways (Fig. 1Bi; *Drosophila*: Agrawal et al., 2020; vertebrates: Azim et al., 2014; Bosco and Poppele, 2001; stick insect: Bässler and Büschges, 1998; Gebehart and Büschges, 2021; locust: Burrows, 1996; Burrows et al., 1988; Endo et al., 2015; Siegler, 1981). Direct pathways between sense organs and motor neurons allow for fast, immediate excitation of motor neurons (Fig. 1Bi, left). In parallel to these monosynaptic connections, polysynaptic pathways, involving interneurons intercalated between sense organs and motor neurons, show a much more diverse profile (Fig. 1Bi, right). The function of polysynaptic pathways may change with the synaptic drive (i.e. excitation or inhibition) they provide to motor neurons – a drive that can either support or oppose the current motor output (Büschges, 1990; Büschges and Schmitz, 1991; Frost and Kandel, 1995; Nagayama and Hisada, 1987; Sauer et al., 1996; Skorupski et al., 1994) – and the type of computation and signal integration that they (or their network) perform [see 'Challenges of (multi)modal proprioceptive integration in distributed networks']. This network architecture enables distributed, parallel processing of proprioceptive and other types of input (Fig. 1Bii). In the following, we will discuss

Glossary

Assistance reflex
Motor response that acts in the same direction as self-generated or inflicted motion of a limb.

Corollary discharge (or efference copy)
Internally generated signals informing the nervous system about self-generated actions, e.g. movements or self-evoked sensory stimuli (for details, see Straka et al., 2018).

Dedicated pathways
In dedicated pathways, signals are transmitted in series along a single pathway, trading off response flexibility for speed.

Distributed networks
In distributed networks, signals diverge onto a number of pathways that process information in parallel and are considered to provide the network with flexibility and context-dependency.

Fictive locomotion
Fictive locomotion can be pharmacologically elicited in *ex vivo* or immobilized preparations; the neural activity follows the pattern of actual locomotion.

Gain
Ratio between signal input and output of a network, e.g. a scaling factor that an interneuronal network applies to a sensory input when generating the motor output.

Lateral connectivity
Neuronal connections within the same layer of a network, e.g. between sensory afferent inputs, or between interneurons of the same processing layer.

(Local) premotor network
Neuronal circuitry controlling motor output and movements, in this case referring to local networks immediately upstream of motor neurons. Local neurons or networks are contained within a single thoracic segment and do not themselves send or receive (but can be the target of) intersegmental ascending or descending inputs.

Multimodal
Multimodal signals are a convergence of multiple sensory modalities (e.g. joint movement and leg loading).

Network topology
Wiring diagram of a neuronal network, either at the level of single cells (the connectivity of each neuron in the network), or at a higher conceptual level (the connectivity of layers and subpopulations of neurons).

Optogenetic manipulation
Light-induced manipulation of, for example, genetically encoded channelrhodopsins to temporarily change the physiological state of a neuron.

Postural reflex
Reflexive response to an internal or external perturbation to maintain the posture of a limb or the entire body (e.g. knee-jerk reflex), often stereotyped motor responses elicited by local circuitry.

Resistance reflex
Motor response that opposes an inflicted motion of a limb to keep it in place.

Unimodal
Sensory signals that originate from the same sense organ, or multiple sense organs encoding the same sensory modalities (e.g. joint movement).

Ventral nerve cord (VNC)
Insect equivalent of the vertebrate spinal cord, containing, among others, local neuronal circuitry for limb movements.

the properties and respective advantages of distributed compared with dedicated pathways (see Glossary). We define dedicated pathways as invariant, 'hardwired' functional pathways in which a given input always results in the same output (Fig. 1Bii, left). Distributed functional pathways are defined as networks in which an input is spread out onto a number of parallel pathways that are amenable to additional inputs, thereby achieving greater flexibility (Fig. 1Bii, right). In other words, a given input to a distributed network might result in different outputs depending, for example, on the behavioral or sensory context. For the sake of discussion, we will treat dedicated and distributed networks as separate concepts; however, they most likely represent opposite ends of a spectrum in which the nervous system may modulate the response of dedicated pathways or stereotype the output of distributed networks.

Dedicated and distributed pathways are defined functionally, and overlap to some degree with the anatomical definition of monosynaptic and polysynaptic pathways. Monosynaptic connections provide fewer opportunities for modulation and hence tend to be associated with dedicated functions, whereas polysynaptic pathways tend to produce more variable outputs owing to the inherent noise of the larger number of neurons involved. Nonetheless, monosynaptic pathways may be modulated, e.g. through presynaptic inhibition (Burrows and Laurent, 1993; Burrows and Matheson, 1994; Clarac and Cattaert, 1996; Dudel and Kuffler, 1961; Sauer et al., 1997), and polysynaptic pathways may be dedicated, e.g. where an intercalated interneuron is simply used to switch the sign of a sensory signal from excitatory to inhibitory (e.g. Burrows, 1989). In this Review, we will therefore distinguish between functional network properties (dedicated versus distributed) and anatomical ones (monosynaptic versus polysynaptic).

The first evidence for a distributed, parallel control architecture in proprioceptive networks originated from initial findings in the cat spinal cord in the 1960s (Jankowska et al., 1967a,b; reviewed in Morton and Chiel, 1994). Since then, it has also been found in insect premotor networks (Burrows et al., 1988; Büschges, 1990; Hess and Büschges, 1997): for example, modeled networks with distributed processing of proprioceptive signals can sufficiently explain the observed motor output of the stick insect leg control system (e.g. Sauer et al., 1996; Stein et al., 2008), as well as locust flight (Ausborn et al., 2009) and leech reflex behavior (Kristan et al., 1995).

The advantages of dedicated versus distributed pathways have long been a matter of debate (see Hooper, 2005). As discussed above, there is no doubt that both types of network architecture are involved in generating the motor output. However, we propose that dedicated circuits are able to contribute only to a specific set of rapid or stereotyped behaviors, e.g. escape responses (see below) or scratching in response to tactile stimuli (Page and Matheson, 2004), whereas a distributed network architecture allows for the flexible and vast behavioral repertoire that most animals are capable of. Dedicated pathways (Fig. 1Bii, left), in which sensory input is relayed monosynaptically or via (a chain of) interneurons to the motor neurons, allow for fast, stereotyped, yet potentially very finely honed motor responses. These mostly invariant reactions to sensory stimuli are useful in situations that do not require further integration of context- or motor state-dependent information for the decision-making and action-selection process. An example of such a response is the escape reflex: once elicited, this overrides most other behaviors and results in a stereotyped neuronal cascade that ultimately produces a fast movement away from the perceived threat (Sillar et al., 2016). Note, however, that there are some mechanisms used by prey to avoid predictability in the escape response – we are not discussing those here (Humphries and Driver, 1970).

Dedicated pathways produce quick, invariant output and are thereby – as the term implies – dedicated to producing a certain output for a given input in a specific behavioral context [e.g. the tail flip of the crayfish escape response (Wine and Krasne, 1972), or the giant fiber-mediated escape jump of *Drosophila*]. As the example of the giant fiber system in *Drosophila* demonstrates, these pathways are often anatomically evolved for speed by involving few neuronal components, large axon diameters and electrical synapses (Allen et al., 2006; Ammer et al., 2022; Augustin et al., 2019). These features increase the transmission velocity of excitation and reduce the synaptic delay, thereby contributing to fast and efficient signal propagation to the muscles involved in executing the escape. Additionally, to reduce the delays imposed by muscle contraction (e.g. Guschlbauer et al., 2007), these direct pathways often target fast motor neurons, thereby enabling rapid motor responses (Gebehart and Büschges, 2021; Phelps et al., 2021). Although dedicated pathways can be beneficial in allowing very rapid responses, the speed of these pathways and their feedforward network architecture does not easily allow for rapid integration of additional information (e.g. another sensory modality) while the movement is ongoing, as would be necessary to correct a movement trajectory, for example. Distributing sensory information throughout a web of interconnected interneurons allows for this sort of integration, thereby facilitating context-dependent sensory processing and adaptive behavioral output (Fig. 1Bii, right). Therefore, a distributed network potentially sacrifices processing speed for flexibility, task-specificity and robustness, and the potential to generate diverse outputs depending on behavioral, sensory and other internal contexts (e.g. Feng et al., 2020; Jiang et al., 2015; Lindén et al., 2022; Lockery and Sejnowski, 1992; Namiki et al., 2022).

A motor network based purely on dedicated pathways would require individual pathways for every possible motor motif and would reduce an animal's behavioral flexibility to that of early robots and simple feedforward software programs (Buschmann et al., 2015). In contrast, relying only on distributed networks might be too computationally intensive or induce delays that are too long in situations in which the survival of the organism depends on speed. We argue that most systems, including those maintaining postural stability, make use of and benefit from a combination of both principles – dedicated, fast pathways for 'hardwired' responses that require little to no modulation, and distributed (albeit slower) networks generating the behavioral variability necessary to cope with unpredictable environments.

Indeed, distributed processing is known to ensure the flexibility of motor output (Driesang and Büschges, 1996; Keller and Heilgenberg, 1989; Lockery and Sejnowski, 1992; Osborn and Poppele, 1992), even at the level of what were originally expected to be dedicated command pathways (Feng et al., 2020; Namiki et al., 2022). Similarly, the escape system of *Drosophila* is more complex than initially proposed, involving parallel systems that endow the system with context-dependent flexibility (von Reyn et al., 2014). Thus, today it is clear that even behaviors seemingly as simple as postural reflexes or as straightforward as escape responses represent the net result of converging synaptic inputs from a multitude of sensorimotor pathways of the premotor network at the level of the motor neuron membrane.

Challenges of (multi)modal proprioceptive integration in distributed networks

Across the animal kingdom, postural reflexes (see Glossary) provide the basis and entry point into our understanding of motor control and sensorimotor processing (reviewed in Deliagina et al., 2012; Edwards and Prilutsky, 2017; Jankowska, 1992; Pearson, 1995; Sherrington, 1906; Tuthill and Azim, 2018). Although body and limb posture control is mediated by reflex activation of muscles both during active movements and in the standing animal, the musculature involved might differ between these contexts. A well-studied example is the reflex reversal, which poses a challenge to the local neuronal circuitry by requiring flexible processing of similar inputs in different behavioral contexts (e.g. when maintaining posture versus during active movements). We will consider the case of reflex reversal from resistance to assistance reflexes (see Glossary) when discussing the functional role of distributed network architecture. Initially, we will focus on resting animals, unless specifically stated otherwise.

Studying the neuronal control of body posture at rest provides insights into the neural pathways and sensory processing in the ventral nerve cord (VNC; see Glossary) under more easily controllable conditions than in an actively moving animal. Resting insects control their body posture by the concerted action of their six legs and the thorax. The individual posture of each leg is controlled locally (within a thoracic neuromere) and intersegmentally (across neuromers) by the VNC; given that posture control occurs in the absence of descending input from the brain, it can be considered as being primarily mediated by the VNC (e.g. Graham, 1979; Vandervorst and Ghysen, 1980) and passive tissue properties, such as muscle stiffness and tendon elasticity (Ache and Matheson, 2013; Dudek and Full, 2006; Guschlbauer et al., 2022; Hooper et al., 2009; von Twickel et al., 2019). Although VNC circuits can be (and – especially in actively moving animals – usually are) influenced by descending inputs from the brain (Emanuel et al., 2020; Martin et al., 2015), the decapitated and resting animal is a useful system for studying local control circuits. In this situation, exteroceptive and proprioceptive sensory signals can be experimentally induced by external perturbations targeted at individual sense organs, and their effect on network processing and motor output can be disentangled from the more complex motor signals arising during locomotion and other active movements. For example, the posture of an insect leg is kept constant against a passive flexion of the tibia of the leg (which might be caused, for example, by a shift in the foliage the insect is standing on) by excitation of tibial extensor and inhibition of tibial flexor motor neurons and muscles, thereby allowing the insect to regain and maintain the original resting posture of the tibia (Bässler, 1993; Burrows, 1996). This intrajoint reflex is paralleled by an interjoint reflex that depends on the motor neurons and muscles of the adjacent proximal joint (Burrows et al., 1988; Hess and Büschges, 1997).

By expanding the concept of unimodal distributed processing, increasing evidence for the distributed processing of multimodal feedback is emerging. Convergence of multimodal sensory feedback onto distributed sets of premotor neurons occurs in a variety of motor systems, ranging from chemosensory and mechanosensory inputs in the stomatogastric nervous system of crustaceans (e.g. Follmann et al., 2018) to the integration of tactile and proprioceptive information in flies, locusts and vertebrates (e.g. Burrows, 1985; Jankowska, 2013a; Tuthill and Wilson, 2016b). In locomotor networks, distinct types of proprioceptive sensory signals, providing information about limb and body movement, position and encountered forces, are integrated with other self-motion-related signals, including corollary discharges or efference copies (reviewed in Edwards and Prilutsky, 2017; Pearson, 1995; Straka et al., 2018).

In vertebrates, type Ia/II and Ib afferents signal proprioceptive movement and load feedback from muscle spindles (type Ia/II) and Golgi tendon organs (type Ib) to the spinal networks that control body posture at rest and during locomotion (Czarkowska et al., 1981; Deliagina et al., 2012; Jankowska, 2013a,b; Jankowska and Edgley, 2010; Windhorst, 2007). The situation is comparable to insect locomotor networks, which integrate proprioceptive information from load-sensing campaniform sensilla and movement-sensitive chordotonal organs and hair plates (Bidaye et al., 2018; Burrows, 1996; Field and Matheson, 1998; Gebehart et al., 2021; Tuthill and Wilson, 2016a,b; Zill et al., 2004). The network topology of premotor circuits involved in insect locomotion (specifically walking) has been studied for decades in larger insects such as locusts, stick insects and cockroaches (for reviews, see Ayali et al., 2015; Bässler and Büschges, 1998; Bidaye et al., 2018; Burrows, 1996); however, recent advances in the fruit fly *Drosophila* allow this work to be performed in a more genetically amenable system (Agrawal et al., 2020; Chen et al., 2021; Mamiya et al., 2018; Phelps et al., 2021). Studies in these flies have already demonstrated a considerable functional overlap with circuit architecture as we know it from larger insects (Agrawal et al., 2020; Chen et al., 2021; for further discussion, see 'Conclusions and future directions').

In the VNC of stick insects, locusts and cockroaches, spiking and nonspiking interneurons form a distributed network that integrates multimodal proprioceptive information (Burrows and Siegler, 1976; Büschges, 1990; Gebehart et al., 2021; Pearson and Fourtner, 1975; Siegler, 1981; Siegler and Burrows, 1983). Whereas spiking neurons rely on action potential generation for signal transmission, nonspiking neurons use graded potentials and graded transmitter release; under natural conditions, nonspiking neurons do not produce action potentials (Hengstenberg, 1977; Siegler, 1984). Although it has been hypothesized that nonspiking neurons are also involved in the distributed premotor circuits of the fruit fly (Agrawal et al., 2020), it is currently unclear whether such neurons even exist in the fruit fly VNC, let alone whether they play a similar role in multimodal proprioceptive integration and leg motor control to that observed in larger species.

Multimodal sensory integration poses a challenge for spiking, nonspiking and mixed networks making use of distributed processing: the same network is required to process sensory information in different behavioral or sensory contexts. A distributed network that is based on spiking neurons might employ rate or timing coding, i.e. encoding information in the number of action potentials, their frequency or the precise time points at which they occur (Enoka and Duchateau, 2017; Sober et al., 2018; Srivastava et al., 2017). Nonspiking networks lack this aspect of temporal precision and the all-or-none output that an action potential provides, and by default rely on analogue signaling that may increase the amount of information that is transmitted and allow for continuous graded control in networks with smaller numbers of neurons (de Ruyter van Steveninck and Laughlin, 1996; DiCaprio, 2004; DiCaprio et al., 2007; Siegler, 1984; Takahata et al., 1981).

There are multiple ways in which context-dependent multimodal integration can be achieved in local networks (Fig. 2). These enable circuits of limited neuron numbers to process input signals from different (proprioceptive) sources, and we here discuss different mechanisms of how this can be implemented at the network level. In spiking, nonspiking and mixed networks, context dependency can be achieved by having distinct, albeit potentially overlapping, subsets of neurons that respond to individual or simultaneously occurring multimodal inputs using a combinatorial code (Fig. 2A; e.g. Follmann et al., 2018). However, a recent study in the premotor network of the stick insect found that distinct proprioceptive modalities are distributed onto the same set of nonspiking interneurons (Gebehart et al., 2021). This type of network architecture does not support the use of a pure combinatorial code unless the weights of its inputs are adapted by changing the gain of individual pathways, a means of achieving context dependency that we refer to as 'gain control' (Fig. 2B; Driesang and Büschges, 1996; Gebehart et al., 2022; see 'Functional insights into the role of gain modulation for distributed processing'). As a third alternative, representing a mixture of combinatorial coding and gain control, distributed networks could be modular, adding or short-circuiting (gating) individual elements or entire sub-networks depending on the behavioral context, for example, by presynaptic or postsynaptic inhibition (modularization, Fig. 2C; Clarac and Cattaert, 1996; Rudomin and Schmidt, 1999). Siegler (1981) found that in locusts, the effect of nonspiking interneurons on downstream motor neurons varies with the leg posture, and Berg et al. (2015) showed that the output of a command-like neuron for searching movements in stick insects is gated when the leg is touching the ground (Fig. 2D). Similarly, evidence suggests that proprioceptive afferent signals are rhythmically shunted (i.e. prevented from reaching the premotor circuit) in locusts during specific phases of walking, presumably to avoid saturating the network (Wolf and Burrows, 1995). These mechanisms are not mutually exclusive, and there is ongoing debate regarding how the premotor networks of different insect species and insects of different sizes are organized. Proprioceptive information on movement is distributed throughout the premotor network of the fly leg, and appears to have some overlap with load-sensitive pathways (see fig. 3 in Agrawal et al., 2020), but it is unclear whether the overlap of distributed networks integrating different proprioceptive modalities is as extensive in *Drosophila* as it is in stick insects (Gebehart et al., 2021).

It will be important to answer these questions if we hope to identify common principles in insect premotor processing, and the underlying computations. In addition, it is still unknown how insect premotor networks solve the 'binding problem' – how do they maintain input identity and information content once multimodal signals converge within a network (von der Malsburg, 1999)? In fact, whether these networks solve the binding problem at all is unknown – once proprioceptive signals from distinct sense organs converge, they might instead merge to form a higher-level representation of the proprioceptive context.

Moving from studies of unimodal to multimodal processing and identifying the mechanisms of multimodal proprioceptive integration in distributed networks are essential steps in understanding how premotor networks manage the barrage of sensory inputs they encounter in natural settings, and, ultimately, in explaining how nervous systems with small numbers of neurons generate the impressive repertoire of insect behaviors. Below, we will use the example of multimodal gain control to highlight some of the functional insights that insect motor systems have provided.

Functional insights into the role of gain modulation for distributed processing

Parallel, distributed processing is found ubiquitously in sensorimotor networks across the animal kingdom. The best-studied cases are neural circuits generating the various reflexes that maintain body posture in the resting organism against external perturbations, i.e. resistance and postural reflexes, either of which can be local (mediated within the same segment; locust: Burrows et al., 1988; *Aplysia*: Hawkins et al., 1981; leech: Lockery and Kristan et al., 1990) or intersegmental (mediated across mutliple segments; crayfish: Jellies and Larimer, 1985; locust: Laurent and Burrows et al., 1989). The distributed architecture of these sensorimotor pathways also allows for their flexible recruitment during diverse active movements such as assistance reflexes (stick insect: Driesang and Büschges, 1996; crayfish: Skorupski, 1992), escape maneuvers (cockroach: Ritzmann and Pollack, 1990), feeding (sea slug: Mpitsos and Cohan, 1986), jumping (locust: Burrows and Pflüger, 1988), uropod movements (crayfish: Nagayama and Hisada, 1987) and leg stepping (locust: Wolf and Büschges, 1995).

A caveat in studying any kind of motor control is the degree to which the invasive procedures required to gain access to the nervous system affect the network's activity, especially when studying the effects of behavioral context on the system. It is therefore important to point out that sensory or proprioceptive responses in most of the

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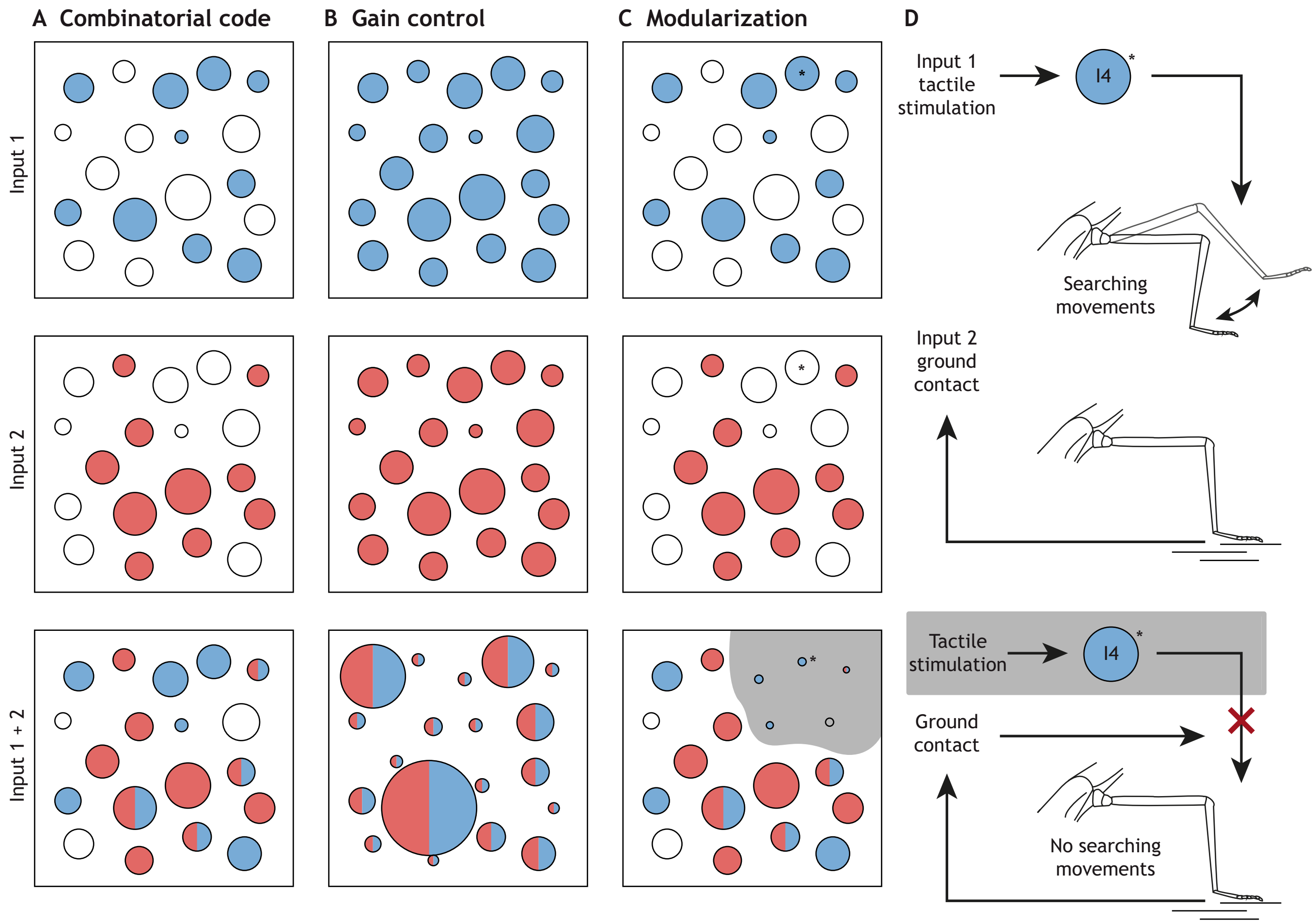

Fig. 2. Mechanisms for context-dependent multimodal signal integration in distributed networks. (A) Combinatorial code. Different, potentially overlapping, subsets of neurons respond to two unimodal inputs (1, top, and 2, middle); multimodal context information can be extracted from the combination of separate sets of neurons being active (1+2, bottom). (B) Gain control. All elements of the network respond to both types of unimodal input. In the multimodal case, the gain of individual network elements is increased or decreased so that the multimodal context can be inferred. Gain change represented by change in dot size. (C) Modularization. Comparable to a combinatorial code as shown in A, but subnetworks are functionally added or removed (shaded area) from the population depending on behavioral context to shape multimodal context-dependent responses. Note that the schematic depicts extreme cases of context-dependent multimodal signal integration that are not necessarily mutually exclusive. (D) Stick insect leg searching movements, an example of network modularization. Upon tactile stimulation, interneuron I4 (*) elicits searching movements (top). In the presence of a second input (ground contact, middle), the effects of I4 activation are blocked and no searching movements occur (Berg et al., 2015). For examples of combinatorial code and gain control, see Follmann et al. (2018) and Gebehart et al. (2022), respectively.

studies highlighted above were elicited in semi-intact preparations in which the nervous system is not removed from the body cavity, but the animal is immobilized to allow for stable neuronal recordings, and only the tested limbs or segments are free to move or respond to the stimulus. If the animal is not actively moving and other system-specific criteria are met, the system is considered to be at rest or quiescent. For the example of the stick insect, these criteria include a lack of phasic motor neuron activity and stereotyped, well-defined reflex responses to external stimuli (Bässler and Büschges, 1998). Actively behaving preparations are much harder to evoke and record from in experimental settings – returning to the example of the stick insect, signs of activity include active movements of non-immobilized body parts such as legs, antennae or the abdomen. These conditions certainly do not reflect the full sensory and behavioral experience of an animal in its natural setting – for example, immobilized animals typically lack the natural loading conditions of supporting their own body weight – and these constraints should be taken into account when interpreting results. However, despite experimental limitations, it is exactly in those transitions from one context to the other – for example, in the switch between resting and actively behaving, or between different types of behavior – that we will be able to unravel how premotor networks might change their mode of operation.

The evidence discussed above suggests that compact premotor networks benefit from a distributed architecture when it comes to flexible sensorimotor processing. The following scenarios highlight mechanisms by which the output of distributed networks is tuned by the behavioral context, shaping the network's output to the current requirements of the motor system. For contextually appropriate postural reflexes and other immediate motor consequences of sensorimotor integration, the relative strength or weighting between opposing and supporting pathways can be modified, altering the gain of the network's output (Fig. 3A,B). In a unimodal context, this has been shown by inducing a change in the current behavioral state of the animal. For example, in locusts, the initiation of (fictive; see Glossary) flight in initially quiescent animals changes postural reflex gain at both the level of the motor output and the distributed premotor network (Büschges and Wolf, 1996). Similar changes in

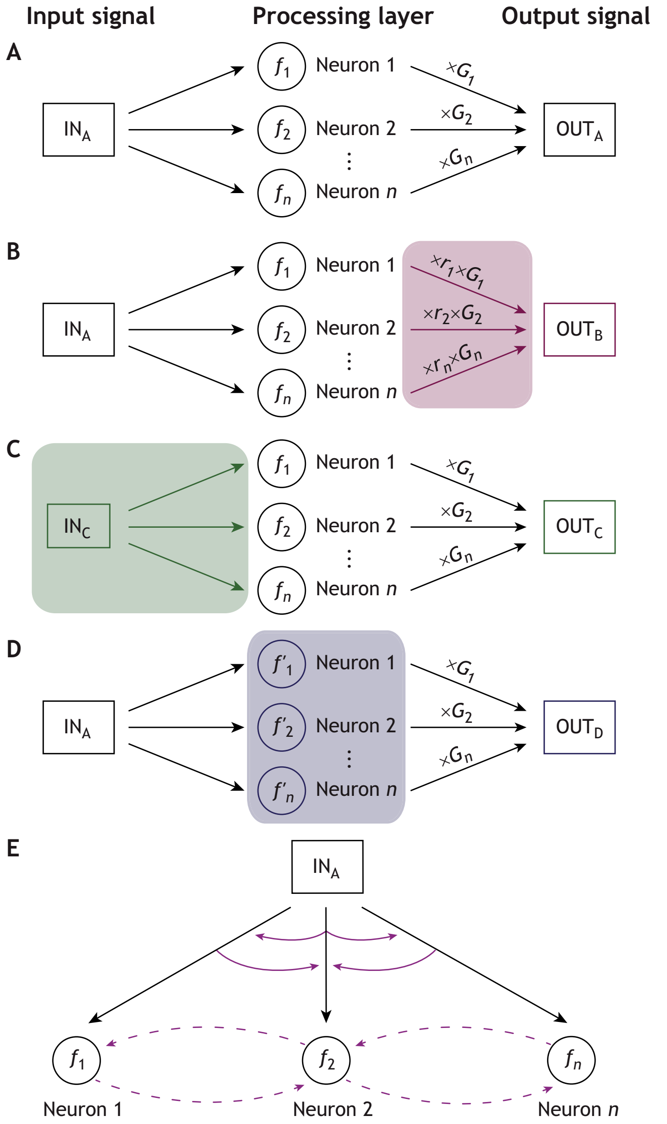

Fig. 3. Changing response gain in a distributed network. (A) Default state. An input (IN) is distributed onto a parallel number (n) of neurons that process signals individually (function f). The output of each neuron is subjected to a set gain (G) before converging onto the network's output (OUT). (B) Changing the gain of individual parallel pathways (r), e.g. strengthening pathways supporting versus those opposing a given behavior in an antagonistic network, can shift the output towards, in this example, supporting the behavior. (C) Gating or changing the input to a network (IN) can affect output gain without altering network processing itself. (D) Altering the computations that individual neurons perform on a given input (f') without altering the input itself can change the output. (E) Examples of potential lateral connectivity within a network. Lateral connections can occur prior to the processing layer, through presynaptic afferent inhibition (purple, solid arrows), or within the processing layer, by reciprocal or unilateral connections among its neurons (purple, dashed arrows).

sensorimotor gain of proprioceptive reflexes occur spontaneously in stick insects (Büschges and Schmitz, 1991), gate command-like signals for searching movements of stick insect legs (Berg et al., 2015), alter the threat response in crayfish (Edwards et al., 2003) and control head movements in crickets (Hensler, 1988).

In addition to changing the weighting between the distributed pathways, a network's response gain can be changed by altering its input (Fig. 3C) or changing how these inputs are processed (Fig. 3D). As mentioned above, clear examples of distributed premotor circuits switching their operational mode are found in motor systems transitioning from a quiescent, immobile or resting state to active movements, including locomotion. Note that 'state' here refers to the animal's level of active movements and neuronal activity. Although the active and resting states are clearly defined in stick insects (see Bässler and Büschges, 1998), it is unclear whether they are distinct or are instead points along a continuum, or how directly they can be compared across animal species.

Changing the sign of reflex action from maintaining a fixed posture to allowing and assisting active movements (which we describe in more detail below) is one of the most drastic examples of switches in premotor network outputs that has been reported for various motor systems, in both vertebrates and invertebrates (locust: Zill, 1985; stick insect: Bässler, 1976; Driesang and Büschges, 1996; crayfish: DiCaprio and Clarac, 1981; Skorupski, 1992; cat: Forssberg et al., 1975; reviewed in Büschges and El Manira, 1998; Clarac et al., 2000). Here, we will highlight the example of the stick insect. When the insect switches from the resting state (i.e. maintaining a fixed posture) to active leg movements, the responses of the circuit to mechanosensory proprioceptive movement signals change. During active movement, joint flexion signals from the femoral chordotonal organ no longer elicit a postural resistance reflex in motor neurons actuating this joint. That is, instead of joint flexion activating tibial extensor and inhibiting tibial flexor motor neurons as it does at rest, ongoing flexion is supported and tibial extensor motor neurons are inhibited (Bässler, 1976, 1988). This reflex reversal is based on a marked change in proprioceptive signal processing in the distributed network of interneurons intercalated between mechanosensory and motor neurons (Bässler and Büschges, 1990; Driesang and Büschges, 1996; Sauer et al., 1996), and is one of the neural mechanisms supporting the generation of leg stance during walking (Bässler, 1986; Bässler and Büschges, 1998; Ekeberg et al., 2004). The underlying modifications in sensorimotor processing include both changes in the gain of individual pathways – leading to a shifted weighting between the supporting and opposing pathways (see Fig. 3B) – and also reversals in signal processing and the resulting output of individual pathways to tibial motor neurons (see Fig. 3D; Driesang and Büschges, 1996).

Taking a multimodal perspective, it is important to highlight a mechanism by which the gain of a signaling pathway can be modulated in a way that depends on the sensory context; concurrent load feedback signals increase the probability of a reflex reversal (Akay and Büschges, 2006). In a similar multimodal sensory context, it was recently shown that proprioceptive integration of load and movement mechanosensory feedback is mediated by a distributed premotor network in the stick insect joint control system. Sensorimotor gain of one sensory input (movement) is altered in the presence of another (load) by shifting the weighting of the antagonistic distributed network, favoring pathways that are opposing, rather than supporting, the ongoing motor output (Gebehart et al., 2021, 2022).

Computational modeling approaches have demonstrated the possibility and efficiency of distributed networks for motor control (Lockery and Sejnowski, 1993; Sauer et al., 1995, 1996; Stein et al., 2008). A recent model implementing stick insect data could also induce a reflex reversal using presynaptic afferent inhibition to control the gain of the insect's distributed sensorimotor pathways (Goldsmith et al., 2021). For a more detailed discussion of the computational approaches to understanding proprioception, see reviews by Dallmann or Pearson and their respective colleagues (Dallmann et al., 2021; Pearson, et al., 2006).

A brief note on network topology

So far, we have discussed the functions of parallel pathways, while neglecting their lateral connectivity, i.e. lateral connections between interneurons of a distributed network (Fig. 3E). Although lateral connections have been found in some insects (locust: Burrows, 1979; stick insect: Gebehart and Büschges, 2021), few data are available on the degree of lateral connectivity between the sensorimotor pathways of premotor networks in the insect VNC. In this regard, electron microscopy datasets of the entire *Drosophila* VNC (Azevedo et al., 2022 preprint; Marin et al., 2023 preprint) will provide a strong starting point for unraveling the details of the circuitry, once the premotor circuits homologous to those in larger insects have been identified and functionally characterized in behaving animals (see Agrawal et al., 2020; Chen et al., 2021).

The two alternatives on the extremes of what might turn out to be a spectrum are sparse versus abundant lateral connections among the distributed pathways. If these networks are only sparsely connected in the lateral axis, it is likely that individual neurons and their responses could be tuned by their upstream partners, but the overall network would consist of independent parallel pathways. Consequently, the outputs of the parallel pathways would be collected, individually weighted and summed at the output stage of the network, i.e. the motor neuron membrane. This is an extension of the concept of dedicated pathways into a distributed network, with the individual neurons or pathways acting as simple signal relay stations.

In contrast, an abundance of lateral connections in the form of recurrent loops would enable computationally more complex contextualization of input signal processing (Tanaka, 2016). Contextualization might take different forms, e.g. shifting of tuning curves, gain modulation, gating or time-delayed signal integration (Büschges and Wolf, 1996; Hedwig and Sarmiento-Ponce, 2017; Jung et al., 2011). Essentially, the activity of each individual neuron would depend on the actions of the network as a whole. Such networks face the danger of escalating ‘runaway excitation’, in which reciprocal excitation of recurrently connected neurons elicits an uncontrolled spiral of excitation that floods the network and essentially incapacitates it (Douglas et al., 1995); thus, the level of excitatory and inhibitory connections within the network should be carefully balanced.

We propose that insect premotor networks, with their limited number of neurons (Bates et al., 2019; Burrows, 1996), might contain abundant lateral connectivity. Furthermore, especially given their restricted network sizes in relation to those of vertebrates, it is possible that insect premotor networks rely even more heavily on the specificity of their (local) connectivity – and the weighting of these lateral connections – either at the level of the interneuronal network through recurrent connections or at the level of its inputs through presynaptic afferent inhibition (Fig. 3E; Clarac and Cattaert, 1996).

Conclusions and future directions

In this Review, we have highlighted the principles and advantages of the distributed proprioceptive integration that is found across different invertebrate systems, often also considering vertebrate counterparts. The sensorimotor circuits of insect model systems such as fruit flies, locusts, stick insects and cockroaches have manageable numbers of neurons that are individually identifiable, allowing for repeated recordings from the same neuron across individuals. These insects are amenable to optogenetic (see Glossary) or mechanical manipulations, and their motor programs can be elicited and analysed in a consistent way. Furthermore, the genetic toolkit of *Drosophila* and the availability of electron microscopy datasets of the entire nervous system – which allow for anatomical dissection and functional prediction of circuits (Azevedo et al., 2022 preprint; Dorkenwald et al., 2021; Scheffer et al., 2020; Winding et al., 2023; Zheng et al., 2018) – provide important research tools for the investigation of motor control in insects. Thus, insects represent an outstanding system in which to unravel the open questions in sensorimotor integration in general, and specifically to investigate the emergence of the sense of proprioception in distributed networks. How is ascending proprioceptive information integrated in the insect brain? Stepping-related signals that originate in the VNC are transmitted all the way into early visual processing neurons in *Drosophila* (Fujiwara et al., 2017), but the number of ascending pathways from the VNC is limited (ca. 2400 ascending neurons in total; Dorkenwald et al., 2023 preprint). Does this imply a greater relevance of dedicated pathways for ascending information? Or do ascending neurons provide parallel, distributed information channels? What are the mechanisms used to balance and tune the gain of individual pathways to adapt them to different behaviors? How is descending control from higher-order brain centers integrated to allow for goal-directed motor control that does not interfere with the current state of the motor system, and how does descending control allow for motor control to be tuned appropriately? Finally, how do distributed networks solve the binding problem for multimodal inputs?

Answers to all these questions will bring us closer to an understanding of the mechanisms for sensorimotor integration in insects and in other animals. *Drosophila*, with its expanding genetic toolkit, has already provided insights into network connectivity and network computations at an unprecedented level of detail, and will continue to do so. However, it is our opinion that this by no means abolishes the necessity for alternative, especially larger, insect model systems. Insects such as locusts, stick insects and cockroaches allow for much more naturalistic, mechanical stimulation and manipulation of sense organs than is achievable using optogenetic activation, for example. Similarly, although these species are not yet (and potentially never will be) as amenable as *Drosophila* to genetic manipulations, their nervous systems are much more accessible to electrophysiological recordings, not only from cell somata but also from the neuronal arborizations in which signal transmission and integration occurs. Technology and experimental methods are evolving and improving at an immense pace, and patch clamp, calcium and voltage-imaging techniques in *Drosophila* yield valuable insights. However, to avoid a situation in which we, as a field, understand in great detail how motor control works ‘in stick insects’ or ‘in *Drosophila*’, we propose that these model systems should be used in parallel, to answer the questions for which they are best suited. It is our hope that emphasizing the importance of diversity in model organisms in the neurosciences will help us to identify general principles of motor control that potentially span the animal kingdom.

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ECR Spotlight

This article has an associated ECR Spotlight interview with Corinna Gebehart.

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