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*Introduction***Information processing in miniature brains****L. Chittka* and P. Skorupski***Queen Mary University of London, Research Centre for Psychology, School of Biological and Chemical Sciences, Mile End Road, London E1 4NS, UK*

Since a comprehensive understanding of brain function and evolution in vertebrates is often hobbled by the sheer size of the nervous system, as well as ethical concerns, major research efforts have been made to understand the neural circuitry underpinning behaviour and cognition in invertebrates, and its costs and benefits under natural conditions. This special feature of *Proceedings of the Royal Society B* contains an idiosyncratic range of current research perspectives on neural underpinnings and adaptive benefits (and costs) of such diverse phenomena as spatial memory, colour vision, attention, spontaneous behaviour initiation, memory dynamics, relational rule learning and sleep, in a range of animals from marine invertebrates with exquisitely simple nervous systems to social insects forming societies with many thousands of individuals working together as a ‘superorganism’. This introduction provides context and history to tie the various approaches together, and concludes that there is an urgent need to understand the full neuron-to-neuron circuitry underlying various forms of information processing—not just to explore brain function comprehensively, but also to understand how (and how easily) cognitive capacities might evolve in the face of pertinent selection pressures. In the invertebrates, reaching these goals is becoming increasingly realistic.

Keywords: behaviour; cognition; ecology; evolution; invertebrate; nervous system

1. INTRODUCTION

In 1959, when computers filled entire rooms (and there was perhaps a perception that better computers would have to fill factory halls), Richard Feynman pointed the way in the direction of miniaturization in information technology. In a lecture famously entitled ‘There’s plenty of room at the bottom’ he asked ‘Why cannot we write the entire . . . *Encyclopaedia Britannica* on the head of a pin?’ (p. 22 in [1]). At the time, the audience might have been equally sceptical as when Darwin, impressed by ants’ ‘wonderfully diversified instincts, mental powers and affections’, proclaimed that an ant’s brain, despite its size being ‘the quarter of a small pin’s head. . . is one of the most marvellous atoms of matter in the world, perhaps more so than the brain of man’ (p. 145 in [2]).

The brains discussed in this special feature are staggeringly small when compared with those of humans; indeed, multiple times smaller than the 2×2 mm voxels (three-dimensional pixels) that form the unit of resolution in common brain imaging studies on humans. Some of the smallest insects’ entire brains are equivalent in size to only a few human neurons [3]. Nonetheless, these brains contain the full circuitry needed for identification of mates, food and oviposition sites, the motor routines to reach these targets, the control to activate the correct behaviour pattern at the right time, and learning and memory [3,4]. Some functions that in primates are

supported by several thousand synchronously active neurons, such as in the dopaminergic reward system [5], can be performed by a single neuron in an insect [6], and miniaturization can be driven further by re-using single neurons as components of multiple circuits [7]. *There’s plenty of room at the bottom.*

Some social insects have behavioural repertoires of the same order of magnitude as some mammals [8]. Perhaps with the exception of the beaver and the human, no mammal engages in the kind of elaborate cooperative home construction found in the insects, including multi-storey ‘buildings’ with intricate substructures for food storage, brood-rearing and climate control—often constructed and operated by highly skilled task specialists [9,10]. And recent years have seen a remarkable surge in studies on cognitive performance in insects, and the possibilities of numerosity [11], concept formation [12], attention-like processes [13] and consensus building in groups [14] are now seriously considered. This special feature is about raising appreciation for the complexity of these phenomena generated by tiny brains, and to attempt a few small steps in the direction of understanding how these feats are underpinned by neural circuits, and their evolution (and their costs) in the economy of nature.

How might it all have begun? Jékely [15] gives fascinating insights into early nervous system evolution. He points out that, while protists’ behaviour is often remarkably sophisticated, fundamental advances were made in multi-cellular organisms by having dedicated sensor and effector cells, connected by a chemical synapse, such as in the larvae of the marine annelid *Platynereis*. Jékely suggests that the larvae of these extant annelids might

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One contribution to a Special Feature ‘Information processing in miniature brains’.

be similar to the most ancestral conditions of animal nervous systems. It is useful here to remind ourselves that nearly all molecular components of neurons, as well as types of plasticity in circuits, are present in vertebrates and invertebrates, and thus presumably in their common ancestor [8].

As nervous systems expanded and elaborated over evolutionary time, they faced increasing costs [16], as well as the challenge to activate circuits appropriate to the behavioural situation rather than simply as a response to adequate stimulus configurations. This means learning about and remembering contexts [13]. But what does this cost? Burns *et al.* [16] discuss the metabolic costs and fitness costs and benefits of brains of varied size, as well as the specific costs of various forms of learning and information storage. As Brembs [17] makes clear, brains, even miniature ones, cannot be accounted for in terms of stimulus–response relationships; instead, behavioural flexibility and selection appear to be fundamental to animals. Flies will spontaneously generate novel behavioural turns in precisely (deterministically) controlled experimental environments [17], showing they are actively probing the environment independently of the causal chains between sensory receptors and motor outputs. Behavioural flexibility is also a major theme in van Swinderen & Andretic's review [13] of the role of dopamine in behavioural arousal in *Drosophila*. Rather than a simple direct relationship between dopamine activity and arousal *per se*, the authors argue for a more sophisticated role, where intact dopaminergic function is required for behavioural selection, with concomitant suppression of irrelevant responses. This leads to the intriguing suggestion that dopamine may be involved in selective attention in flies [13].

Many of the high-profile studies on cognitive capacity in invertebrates have been on social bees (e.g. the contribution by Avarguès-Weber *et al.* [12] and references therein). It is therefore tempting to assume that the complexities of social life have favoured the evolution of 'insect intelligence'. This 'social brain hypothesis' [18] was originally proposed for the insects in 1850 by Dujardin [19], who discovered that the mushroom bodies (dorsal structures in the insect brain now known to be engaged in learning and memory) were substantially enlarged in the social insects compared with solitary ones, and concluded that they are the seat of intelligent control, or indeed free will, in the insects. Farris & Schulmeister [20] have now carefully evaluated mushroom body architecture in a wide range of Hymenopteran insects, and mapped their lifestyles and neural structure onto an established phylogeny. They found that insects at the base of the tree oviposit on leaves, and their mushroom bodies are small, simple in structure and, just like in ancestral insects, receive only olfactory (but not visual) input to the calyx region of the mushroom bodies. However, relatively enlarged mushroom bodies, with elaborate structure and visual as well as olfactory inputs, evolved not with sociality but around 90 Myr earlier. The ancestors of today's social insects were all parasitoids—solitary wasps that often paralyse prey to be consumed alive by their larvae—and it is this lifestyle that apparently necessitated mushroom body elaboration. The challenges of locating and overwhelming adequate prey (beautifully described in the *Souvenirs entomologiques* by Fabre [21] in 1879), as well as larval provisioning and spatial

orientation needed to locate one's nest, presumably placed much higher cognitive demands on these parasitoids than their vagabond, herbivorous ancestors.

Ammophila campestris digger wasps, for example, tend multiple nests at any one time, and meticulously keep track of which ones already contain an egg, which ones have been provided and how recently, and whether a nest has been sealed for good [22]. Fabre already pointed out the remarkable between-species variation in parasitoid behaviour hunting strategies—for example, wasps that hunt insects where the three thoracic ganglia are fused give only one venom injection, whereas wasps that hunt the more typical insects with three separate ganglia will inject each ganglion separately [21]. In this special feature, Hoedjes *et al.* [4] describe how memory capacity and memory dynamics are tailored precisely to each species's needs to store information over various time scales. Indeed it is in the context of suitable food and prey identification that many of the cognitive feats of insects have been discovered [8,12,23]—but the challenges involved might be the same in principle for solitary as for social foragers. The added challenges that came with sociality, almost 100 Myr later, might not have required a fundamental reorganization of the brain, but only minor rewiring of circuitry. For example, the remarkable ability of some wasp species to recognize other individuals of the colony by facial patterns [24] is quite possibly based on more ancestral pattern recognition skills in the context of prey recognition; and indeed it turns out that there are no discernable differences in the neuropiles of the visual systems of these species compared with related species in which face recognition does not occur [25]. Neuronal network analyses confirm that a basic circuitry for reliable face recognition requires only a few hundred neurons and could thus be easily accommodated in the insect visual system [26]. Likewise, in an attempt to identify a neural correlate of the honeybee 'dance language', no 'dance-specific' sensory projections were found in the brains of honeybees when compared with other species that lack the dance [27]. This emphasizes that even seemingly major evolutionary behaviour innovations might be generated by relatively small adjustments in neural circuitry controlling the sequence of muscle contractions that constitutes a behaviour pattern [15,27]. There is no question that interactions between members of insect societies are simpler than in primate groups—it is perhaps unlikely that, in the insects, we will find instances of theory of mind, for example, or tactical deception. Nonetheless the insects clearly demonstrate that it is possible to generate cohesive societies of thousands of individuals by perhaps relatively simple rules—which goes to show that numbers of individuals are not useful as indicators of societal complexity or the cognitive demands involved.

Dyer *et al.* [23] consider the neural mechanisms of visual information processing in bees, their temporal properties and their constraints in decision-making. A major unresolved question in psychology concerns the relationship between sensory input (which is often understood in some detail) and conscious perception via sensory input (which is poorly understood). A conventional view is that to perceive something is to generate a mental representation of it, which is usually taken to be based on an entirely internal neural representation [28]. An alternative view is that perception is based upon

action rather than internal representations [17,29]. To perceive something is to actively sample it, and the perception is constituted in implicit knowledge (accumulated both phylogenetically and ontogenetically) of how the properties of the sensory motor apparatus result in changes in the sensory input during perceptual sampling (for example, eye movements in humans). This account places more of the burden of perception in the world itself, rather than in putative mental representations [30].

Certainly, there is considerable evidence for an intimate connection between perception and action in insect vision [31]. Spontaneous turning movements in tethered flies could be conceived of as active visual probing of the environment, and the perception-as-action perspective fits comfortably with studies on spontaneous actions and decision-making with small brains [17]. In addition, elaborate internal representations of the world are not needed according to this perspective, since the world itself serves as an ‘outside memory’ [29]; this would appear advantageous for small-brained animals, especially those displaying cognitive feats once thought to be the prerogative of primates [12].

What, then, are the advantages of bigger brains [16]? Perhaps the notion of representation, loosely defined, may still be indispensable for understanding the neural basis of perception and action, in which case the question may come down to a matter of representational capacity. For example, humans can take in complex visual information at a glance (in scenes presented for 10 ms) [32], and salient features can ‘pop out’ as a result of rapid parallel processing. In bees, by contrast, preliminary evidence suggests that visual search is strictly serial [33]. It could be, then, that bigger brains buy their owners time: time to do off-line processing. For example, rapid visual categorization (‘at a glance’) in primates implies a time course that seems compatible with only a single sweep of sensory information along the known delays of the visual system [34]. It could be that a single sensory snapshot is less useful for a miniature brain simply because there is less capacity for off-line processing (processing involving significant neural delays)—in which case animals with miniature brains would be constrained to live closer to real time. In active perception, the time taken to build up a picture of the world will depend on how much can be sampled at once, and in a miniature brain there may be less capacity to process a single ‘sensory snapshot’, and consequently a greater dependence on continuous online sampling of the scene. It is possible that reduced representational capacity may lead to fundamentally different perceptual sampling strategies in large and small brains. However, in certain highly active miniature-brained animals such as flies and bees, reduced representational capacity may be compensated by higher real-time sampling of the world [35,36]. As we are approaching an age where the understanding of complete neural circuitry of entire insect brains is within reach [37], answering these questions on a mechanistic level is becoming increasingly realistic.

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