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Are Bigger Brains Better?

Review

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Attempts to relate brain size to behaviour and cognition have rarely integrated information from insects with that from vertebrates. Many insects, however, demonstrate that highly differentiated motor repertoires, extensive social structures and cognition are possible with very small brains, emphasising that we need to understand the neural circuits, not just the size of brain regions, which underlie these feats. Neural network analyses show that cognitive features found in insects, such as numerosity, attention and categorisation-like processes, may require only very limited neuron numbers. Thus, brain size may have less of a relationship with behavioural repertoire and cognitive capacity than generally assumed, prompting the question of what large brains are for. Larger brains are, at least partly, a consequence of larger neurons that are necessary in large animals due to basic biophysical constraints. They also contain greater replication of neuronal circuits, adding precision to sensory processes, detail to perception, more parallel processing and enlarged storage capacity. Yet, these advantages are unlikely to produce the qualitative shifts in behaviour that are often assumed to accompany increased brain size. Instead, modularity and interconnectivity may be more important.

> "*It is certain that there may be extraordinary activity with an extremely small absolute mass of nervous matter; thus the wonderfully diversified instincts, mental powers, and affections of ants are notorious, yet their cerebral ganglia are not so large as the quarter of a small pin's head. Under this point of view, the brain of an ant is one of the most marvellous atoms of matter in the world, perhaps more so than the brain of man.*"

Charles Darwin 1871 [1].

Introduction

In computer technology, no one would seriously suggest that a bigger computer is automatically a better computer. Konrad Zuse's 1940s Z3 computer measured about 2 x 2 x 0.5 m and weighed a ton, but could perform only basic arithmetic operations [2]. In terms of processing power it might easily be out-competed by any of today's programmable pocket calculators. It is the technology within which matters, not the size. The same principle applies to brains. This was recognised early in invertebrate neuroscience: in 1850, Dujardin [3] hypothesised that the 'mushroom bodies' — distinctly shaped, dorsal brain areas in arthropods (Figure 1) — must be the 'organs of intelligence', in part because these areas are relatively enlarged in the social insects. In 1929, Pandazis [4] considered that the biggest mushroom bodies are actually found in horseshoe crabs, despite these animals' low level of 'spiritual life'. He concluded, however, that size doesn't matter: what distinguishes the insect mushroom bodies from those of *Limulus* is that only the former contain cells with extensive dendritic ramifications and connections to all major centres of the brain, as required for a centre of higher-order information processing [4].

Just as in computer hardware, variation in brain size (volume or mass) across animals is extreme: a whale's brain can weigh up to 9 kg (with over 200 billion neurons), and human brains vary between 1250 and 1450 g (with an estimated neuron number of 85 billion neurons) [5,6]. A honeybee's (*Apis mellifera*) brain has a volume of ~1 mm^3 and contains fewer than a million neurons [7,8] (Figure 1). The best single predictor of brain size is body mass [6,9,10] (Figure 2), but whether brain size is an equally good predictor of behavioural repertoire and cognitive capacity is controversial. There are dozens of published correlations between various derivatives of brain size (or sizes of certain parts of the brain) and various indicators of 'intelligence', cognitive capacity, behavioural repertoire, innovativeness and social systems [11–15]. However, there are also numerous fundamental complications with such correlations, which are in part conceptual (for example, correlations never prove causality) [12] and in part arise from rigorous empirical work showing that in many cases such correlations are absent or at least not straightforward [9,12,16]. Perhaps one of the biggest obstacles to correlating brain size with behavioural ability arises when one considers the insects, especially the social ones. Darwin recognised this (see verbatim quote above) and compared bees' skills at 'imitation' and 'understanding' with those of primates [17].

This might seem overly generous, but nevertheless we shouldn't be dismissive of insect's often impressive abilities *just because* they have small brains. As an example of the many tautologies characteristic of the field, Pearce [18] argued that learning speed cannot be used as a measure of intelligence — because the honeybee's speed at colour learning is not just superior to human infants, but to all vertebrates that have been studied. There may be good reasons to be uncomfortable with equating learning speed with intelligence, but that large-brained mammals don't top the chart should not be one of them. Bees' orientation abilities, for example, have to be tailored to a lifestyle of central place foraging, where individuals fan out from the nest over areas measuring several square kilometres to search for flowers; within these areas they can memorise the locations and reward profitabilities of multiple feeders [19], linking them in repeatable stable orders [20,21], memorising which feeder is rewarding at what time of day [22,23], using spatial position as a contextual cue to specific sensory-motor contingencies [24], learning landmark sequences and linking vector instructions to landmarks [25,26]. Foraging from flowers requires the successful identification and classification of the sensory signals that identify the most rewarding targets, and indeed in this context bees display several cognitive abilities previously attributed exclusively to 'higher' vertebrates, including, for example, simple forms of rule learning and categorisation [7,27].

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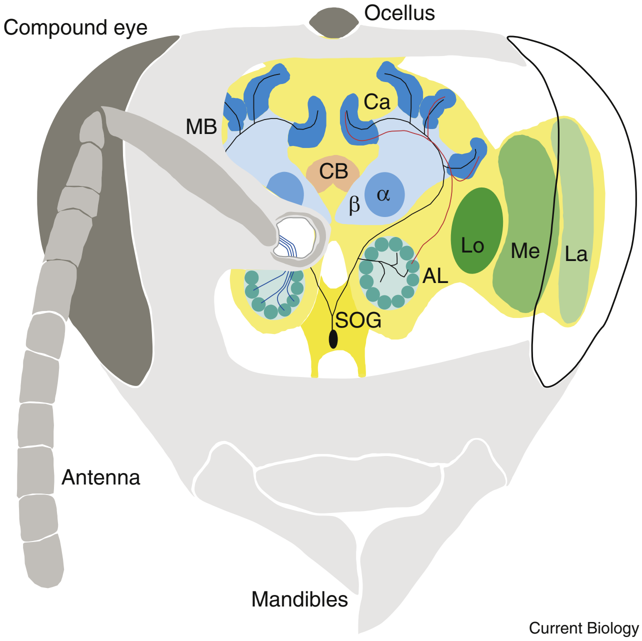

Figure 1. Frontal view of a honeybee worker's brain.

The optic lobes contain ∼216,000 cells each; the lamina (LA), medulla (ME) and lobula (LO) contain a variety of low-level feature detectors, such as colour opponent neurons, motion detectors, edge detectors, and polarisation sensitive neurons. They send projections to the protocerebrum. The mushroom bodies (MB; ∼170,000 cells each) are the primary sites of learning and memory; its calices (Ca) contain segregated regions for olfaction, vision and mechanoreception. The α and β lobes are the mushroom bodies' output regions. The remainder of the protocerebrum contains ∼19,000 neurons, some of which project to pre-motor centres. The protocerebrum also contains the central body (CB), plus neurosecretory cells. The deutocerebrum contains about 2500 motor neurons and, in the antennal lobes (AL), about 4500 neurons subdivided into ∼160 glomeruli. Some 60,000 odorant receptor cells are distributed along the antenna. These belong to several different types, each responsive to a different set of chemicals. Axons from like receptors project to one or a few glomeruli (shown in a 'telephone dial' arrangement inside the antennal lobes). Axonal projections (shown in orange in the right AL) extend from the antennal lobe to higher processing centres, such as the mushroom bodies (MB). The suboesophagal ganglion (SOG) contains VUMmx1, a 'value system' neuron with wide ramifications throughout the olfactory system (shown in red); it represents the sucrose reward pathway for olfactory learning. Figure modified after [7]; cell numbers from [8].

In some insects, social structures are in part based on individual recognition of nestmates [28,29], and recent studies indicate surprising social learning abilities [17], for example mate-choice copying in the fruit fly *Drosophila melanogaster* [30]. No-one familiar with the repertoire of 'instinctive' behaviour patterns of ants and bees would question that it is hard to find parallels in the vertebrate world — consider nest architecture, symbolic communication, nest climate control, large repertoires of chemical communication signals, complex strategies of consensus building, and unique behavioural adaptations, such as slave-making, agriculture and well-coordinated territorial wars [31]. These observations raise two major questions: How do insects generate such diversity and flexibility of behaviour with so few neurons? If so much can be achieved with relatively little neuronal hardware, what advantages are obtained with bigger brains?

Brain Size and Sensory Systems

While *some* increases in brain size will affect cognitive capacity, many increases in certain brain areas — especially those involved in sensory and motor processing — produce only quantitative improvements: more detail, finer resolution, higher sensitivity, greater precision — in other words, *more of the same*. Consider the visual system. The compound eye of the fruit fly *D. melanogaster* has 700 functional units, the ommatidia [32]. Within insects, larger species typically have larger eyes with higher spatial resolution; a large dragonfly can have as many as 30,000 ommatidia [33]. However, the human fovea (a tiny section of less than 1% of the retina) alone contains 60,000 cone photoreceptors [32]. The complete human retina can resolve ∼400,000 'pixels', three orders of magnitude greater than the fruit fly [34].

Crucially, if the added resolution and number of 'pixels' is to be of behavioural relevance, it needs to be processed — in other words, the neural machinery downstream of the photoreceptors needs to expand with the number of receptor inputs from the retina. Insects and vertebrates have convergently arrived at similar solutions to process information within and beyond the visual periphery — retinotopic neural maps, consisting of local neuronal circuits arranged in 'cartridges' or columns that are repeated hundreds or many thousands of times over, depending on the number of inputs from the retina [32,34,35]. These repetitive circuits contain a variety of feature detectors, such as colour opponent neurons, and brightness, edge and motion detectors [36–38], which will have to increase in number (although not always linearly and not in the same proportions) with the number of 'pixels' analysed. The primary visual cortex in mammals, largely engaged in low-level visual feature extraction, thus increases drastically with eye size — in mice, for example, the area is 4.5 mm^2, in macaques 1200 mm^2 and in humans 3000 mm^2 [39] — without necessarily increasing the diversity of ways in which information is processed. The receptive fields of neurons in central neuropiles within the insect visual system, such as the lobula, also contain neurons with receptive field properties that closely resemble those of complex and hypercomplex cells within the first visual cortical area of vertebrates [36,37].

In addition to the increased spatial detail in larger eyes, there are also important differences in processing speed. Larger fly species possess larger photoreceptors with greater numbers of inputs (microvilli) and faster membranes that support higher rates of information processing than the smaller photoreceptors from their smaller counterparts [40]. Indeed, large insect photoreceptors can respond to frequencies far beyond the typical range of mammalian photoreceptors [32,40]. For the higher frequency information obtained by larger photoreceptors to influence behaviour, neurons at each processing stage between sensory receptors and motor neurons must be capable of transmitting and processing higher frequency information. These neurons require dendrites and axons with increased axon diameters and synapses capable of supporting higher rates of vesicle release [40,41] — again, a reverberation of size differences from the sensory periphery through to several subsequent stages of information processing. Increases in the size and number of photoreceptors improve temporal and spatial resolution and, in turn, allow for more detailed images that can be updated more rapidly only if the eyes are supported by suitable neural circuitry to evaluate the added detail. Storing more detailed images in memory will again require more neural substrate — but there is no *a priori* reason to assume that any of this added detail comes with any novel or more advanced forms of information processing.

The principle of repetitive, modular organisation occurs in several areas of the brain, not just those engaged in vision. In another remarkable case of convergent evolution between insects and vertebrates, the peripheral processing of olfactory information follows similar principles across these taxa [42–44]. Typically, in both vertebrates and insects there are approximately as many receptor cell types as there are olfactory receptor genes. Axons from like receptor cells — those that express the same receptor protein and therefore bind the same odorants — project to one or a few glomeruli (Figure 1), globular, anatomically distinct subunits within the antennal lobe (in insects) or the olfactory bulb (in mammals). Individual chemicals reliably activate sets of identified glomeruli [42–44]. Neurons innervating these dense regions of neuropile sum up the inputs from the same chemoreceptors, increasing the signal-to-noise ratio and overall sensitivity, and thus facilitating reliable odorant detection. In insects as well as mammals, glomeruli coding for similar substances are located close together, while those that code for distinct scents are spatially segregated — generating a neural ‘odour map’ [42–44].

As in the peripheral visual system, the vertebrate peripheral olfactory systems contain greater numbers of neurons and olfactory processing centres than those of insects. The common fruit fly has 43 glomeruli within an antennal lobe whilst honeybees have ~160 [7,45]. Humans have ~350 glomeruli in each half of the olfactory bulb, and mice have ~1000 [44,46]. Thus, although insects have fewer glomeruli and presumably, therefore, have a reduced odour space in comparison to many vertebrates, differences in peripheral circuits are quantitative rather than differing fundamentally in the diversity of types of neuronal computation performed.

The motif of scaling of sensory function (and accessory structures) with body size is likely to be repeated in other sensory modalities. Larger animals have larger surface areas whose somatotopic mapping will (all else being equal) require larger corresponding brain areas [10], although, in insects, somatosensory maps occur in the periphery: in the desert locust, *Schistocerca gregaria*, the projections of leg exteroceptors are organised in a somatotopic map within the thoracic ganglia of the ventral nerve cord [47]. Although this mapping is reminiscent of the somatotopic mapping of body surface within the somatosensory cortex of vertebrates, inputs to the map from the body surface are sparser. However, maps for individual limbs remain separate in the locust, rather than being coalesced into a single map in the brain [47].

In conclusion, larger animals possess larger sense organs, which in turn facilitate a more detailed mapping of the world around the animal, provided these sense organs are accompanied by central neural circuits that process the peripheral information. Larger numbers of neurons may increase redundancy, thereby facilitating greater functional diversification of neurons. Increases in the number and size of neurons increase the total energy consumption and reduce the energy efficiency of information processing [41]. Larger neurons are less efficient than smaller neurons irrespective of the rate at which they are transmitting information [41]. Thus, there are severe penalties for excess capacity that promote the reduction of neural structures to a functional minimum. Increases in the number or size of neurons in one region of a sensory system must affect processing in higher-order processing centres and influence behaviour if they are to be maintained during evolution. By default, however, there is no reason to assume that improvements in the quantity of sensory processing necessarily result in higher ‘intelligence’. Another crucial point is that sensory structures and the *absolute* number of receptors and subsequent neurons determine the quality of a sensory system. Thus, although comparative studies almost invariably use relative brain volume, it is primarily the absolute, not relative number of neurons, their size, connectivity and the available energy that affect information processing within the nervous system.

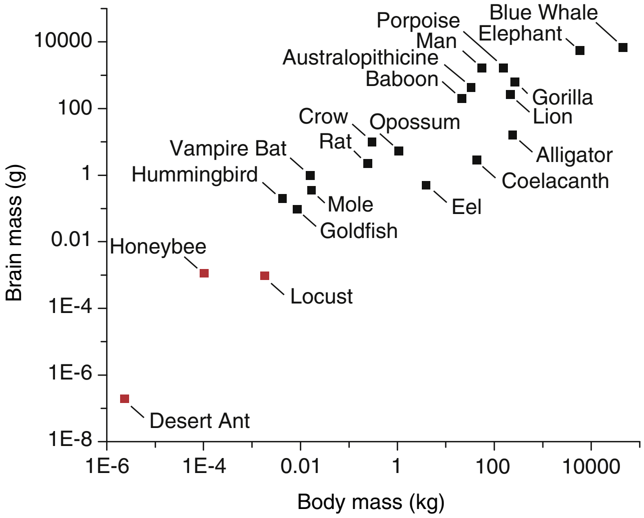

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Figure 2. Body mass is a predictor of brain mass in animals.

The absolute brain mass of insects is considerably smaller than that of vertebrates. Data from representative vertebrates are shown in black, insects in red. Data for vertebrates and ants from [18,93]. Because the mass of the honeybee brain was not available, it is estimated here from volume [7]. (Data for the locust: J.E.N., unpublished.)

Behavioural Repertoires and Scaling in the Motor System

Before we turn to cognitive abilities (which are often difficult to compare between species), we briefly inspect motor repertoires. As Changizi [48] puts it, a “*system… is more complex if it can do more kinds of things*”. Hence it is interesting to compare the numbers of distinct, recognisable motor routines in insects and other animals — the types of behaviour an ethologist might record in an ethogram. In Changizi’s compilation of data on behavioural repertoire size across several dozen species across the animal kingdom [48], the number of different behaviours in various insect species ranged from 15 to 42; amongst mammals, North American moose were listed with 22, De Brazza monkeys with 44 and bottlenose dolphins 123.

We suspected that social insects might have especially rich repertoires; the honeybee, for example, builds hexagonal honeycombs, manipulates powdery substances (pollen) to glue them onto special places on its body, has a variety of repetitive motor patterns (‘dances’) to communicate the location of food, can manipulate and sting opponents while avoiding being stung, cleans the nest of debris, warms the brood by shivering, etc. Our literature survey found 59 distinct

Box 1

Behavioural repertoire of the honeybee worker.

An overview of distinct and (at least in part) hard-wired behaviour patterns that excludes simple motor patterns, such as locomotion, or various types of inactivity.

1. **Aggressive flight:** irritated bees fly at intruder with distinct pitch, preceding stinging [22].
2. **Alarm fanning:** bee stands with abdomen raised, pheromone is released, sting extended; wings whirred [22].
3. **Antennation:** mutual antennal contact between workers without food transfer, e.g. to assert hive membership [129].
4. **Attend dance:** following dancing bee to obtain information about target location [129].
5. **Attend queen:** being part of the queen's 'entourage', at times licking or antennating her [129].
6. **Biting an intruder:** intruders are sometimes not stung but bitten [130].
7. **Beg food:** antennating another worker's head to solicit food [129].
8. **Brief piping:** a signal by dance followers inducing termination of dance [131].
9. **Brood incubation:** pressing body against brood cell and heating, using thoracic muscles [132].
10. **Build comb:** shaping of newly secreted wax into cells; worker, male and queen larvae require different cell sizes, thus different motor routines are needed for construction [129].
11. **Buzz run:** in bee swarm cluster, a specific mode of running through the cluster to signal and induce the swarm departure [133].
12. **Cap brood:** sealing cell with larva about to pupate [129].
13. **Cell cleaning:** removal of debris from empty honeycomb cells [134].
14. **Chew at pollen on worker:** chewing at pollen in another bee's pollen baskets [129].
15. **Chew on hive:** using mandibles to chew on walls surrounding combs [129].
16. **Colony fission:** large number of workers leaves old hive with old queen to relocate into new home. Process and its preparation involves multiple stereotyped individual behaviours [134].
17. **Corpse removal:** removal of dead bees from the hive [135].
18. **Dorsoventral abdominal vibration:** standing bee vibrates abdomen up and down, often while holding on to another worker, in preparation for greater activity levels [129].
19. **Egg laying:** laying unfertilised egg into brood cell [134].
20. **Expulsion of drones:** at end of summer, drones are bitten and dragged out of the hive by workers, sometimes also stung [136].
21. **Extend mouthparts:** extending proboscis to ripen a small drop of nectar [129].
22. **Fan wings:** ventilation of hive by fanning the wings [129].
23. **Feed larva:** inserting head into larval cell to provide food [137].
24. **Feed queen/worker:** regurgitating drop of nectar which receiver imbibes [129].
25. **Get fed:** extending proboscis between mandibles of other worker to receive nectar [129].
26. **Get groomed:** Standing with extended wings to be cleaned by mandibles of other bee [129].
27. **Groom self:** cleaning self with mouthparts or legs [129].
28. **Groom worker:** cleaning hive mate with mandibles [129].
29. **Guarding:** at hive entrance, inspect landing individuals and attack possible intruders [130].
30. **Inspect brood cell:** inserting head into larval cell to inspect a larva [129].
31. **Inspect potential nest sites:** probing cavities for suitability [137].
32. **Lateral shake ('cleaning dance'):** standing worker shakes her body from side to side; this often results in grooming by another bee [129].
33. **Mouth wax — capped cells:** worker walks over capped brood, or capped food reserves, touching the wax with rapid mandibular movements [129].
34. **Nectar foraging:** imbibing nectar from flowers [22].
35. **Nectar storing:** in-hive worker receives food from forager and deposits it in nectar cell [134].
36. **Orientation flights:** flights around hive to learn its landmark surroundings [138].
37. **Packing pollen:** tight packing of pollen into special pollen cells [137].
38. **Piping in swarms:** occurs in the preparation of lift-off to a new hive location [139].
39. **Pollen foraging:** requires the collection of powdery pollen from flowers, grooming it off body surface and packaging into specialised hairy structures on legs (pollen baskets) [22].
40. **Preventing queen fights:** when new queens are raised, workers use multiple tactics to keep them apart [137].
41. **Resin foraging:** collecting resin from trees and transporting it in 'pollen baskets' to the hive, to be used as 'glue' [22].
42. **Resin work in hive:** sealing holes and cracks in hive [22].
43. **Robbing other hives:** the intrusion into other beehives to steal nectar [136].
44. **Round dance:** motor routine indicating to others that there is food in vicinity of hive [22].
45. **Scouting for food:** search for suitable flower patches to recruit others to exploit these [134].
46. **Searching for nest sites:** bees of a swarm search the environment specifically to assess potential nesting sites [134].
47. **Sickle dance:** occurs at the transition between round dance and waggle dance [22].
48. **'Sterzeln':** raising abdomen, release attractive pheromone, and fan wings [22].
49. **Stinging:** attacking and stinging an animal that is perceived as an intruder [136].
50. **Streaker guidance:** informed scouts guide swarm to new nesting site by performing conspicuous flights at top of swarm [140].

51. **Swarm cluster formation:** after colony fission, a swarm settles for a temporary bivouac, for example on tree, to search for new home [134].
52. **Tremble dance:** peculiar 'twitching dance'; signalling function controversial [141].
53. **Turn-back-and-look behaviour:** stereotypic flight behaviour to memorise appearance of new food source or hive entrance [142].
54. **Uncap brood:** using mandibles to remove capping material from brood cell [129].
55. **Unload pollen:** worker scrapes pollen off legs, and into a storage cell [129].
56. **Waggle dance:** figure-eight shaped repetitive run, indicating location of food source [22].
57. **Water collection:** bees seek out freshwater to imbibe and bring back to the hive [22].
58. **Water cooling:** to prevent overheating, water spread over comb; fanning for evaporation [22].
59. **Worker policing:** removing eggs that have been laid by other workers [134].

behaviour types (Box 1). The million-fold increase in a large mammal's brain relative to an insect's does, therefore, allow these mammals to do more 'kinds of things' — about two to three times as many, according to this survey. This is hardly the kind of difference between insects and mammals that might be expected, given the enormous differences in neuron numbers. There are obvious complications with such ethograms — behaviour can be classified at many different hierarchical levels (for example, 'leg extension', 'escape response' and 'brood care' are not equivalent behavioural classifications) — but the behavioural repertoire sizes above were collated by almost as many researchers as there were species, hence a bias favouring insects is unlikely.

One might also argue here that meaningful comparisons of brain size and behavioural ability are only possible between closely related species; this is true if one wishes to trace evolutionary adaptations to particular lifestyles and identify potentially homologous behaviours, but in a broader framework *any* animal, irrespective of body size, should be under pressure to minimise the amount of energy it expends on nervous tissue [41]. So if it is possible to generate a large behavioural repertoire with an insect brain, then why can't the motor centres in brains of larger animals be similarly small, given that brain tissue is extremely costly to maintain [49]?

The observation from sensory systems that some components of bigger brains might add relatively little in terms of number of types or diversity of neuronal operations is repeated in the motor system. For example, homologous neurons in the sympathetic nervous system have less extensive dendritic arbours and receive fewer synaptic inputs in smaller mammals than in their larger counterparts [50]. On average, larger animals will need bigger muscles, and thus possibly greater numbers of motor neurons and axons with larger diameters to cover longer distances in the nervous system. There is, of course, evidence that increased precision in motor skills is correlated with increases in the corresponding motor cortex area's size [51]. Beyond that, there is little clear evidence that the insect motor system has a fundamentally simpler architecture than that of large-brained mammals. *Locusta migratoria* has 296 muscles [52] — more than rodents and almost as many as the 316 present in primates [53] (Figure 3). Insects often outperform vertebrates in terms of the speed of movements, though many of these movements are ballistic and are controlled, at least partly, by cuticular mechanisms [54,55]. Insects can produce extended behavioural sequences, such as the waggle dance of bees [22]. Just as in vertebrates, these behavioural sequences can be reduced to a coordinated series of precisely timed muscle contractions [56]. The architecture of the motor system is similar in insects and vertebrates [57]; both include descending pathways that control the activity of central pattern generators for the generation of rhythmic motor patterns that can be modified by sensory feedback [58]. Both also have local reflexes, triggered by sensory inputs, which can be modified by ongoing behaviours.

The most basic behaviour generated by the motor systems of both vertebrates and invertebrates is the local reflex [56]. Many neurons identified in the vertebrate spinal cord for the generation of limb reflexes have analogues in the insect ventral nerve cord. For example, proprioceptive afferents monitoring limb movements make direct excitatory synaptic connections to the motor neurons generating those movements and to local inhibitory interneurons (1a interneurons in cats, midline spikers in locusts) [59,60]. Thus, although the spinal cord of large vertebrates contains many times more neurons than an insect ventral nerve cord, the circuits generating local reflexes are similar.

Although many motor neurons and muscles may be active in a particular behaviour, relatively few neurons may be necessary to recruit them in a specific order. For example, the neural circuits that generate the flight motor pattern in desert locusts include 72 motor neurons innervating 34 muscles [60]. In comparison, the flight central pattern generator consists of just three neurons, though additional interneurons and sensory neurons are involved in controlling wing movements and adjusting them to prevailing environmental conditions. Relatively few interneurons may be necessary to produce novel behaviours using existing interneurons, motor neurons and muscles. For example, few additional interneurons may be necessary to recruit components of existing motor circuits for limb control to generate the movements necessary for mate attraction in male grasshoppers [61]. Thus, novel behaviours could arise by small numbers of neurons using the basic architecture of motor neurons and muscles but recruiting them in a different order.

Motor neurons in vertebrates are sites of convergence, ensuring their activation occurs only under concerted firing of large numbers of pre-synaptic neurons. In the insects, fewer pre-synaptic neurons, many of which are non-spiking ('analogue'), activate motor neurons [60]. Muscles in insects are also innervated by fewer motor neurons than in vertebrates — typically, tens to hundreds of motor neurons innervate a vertebrate limb muscle [62,63], whereas even highly innervated muscles in insects have fewer than fifteen [64,65]. The increased number of motor neurons innervating muscles in vertebrates might produce increased precision of their movements relative to those of insects, but experimental evidence is absent. However, comparison between

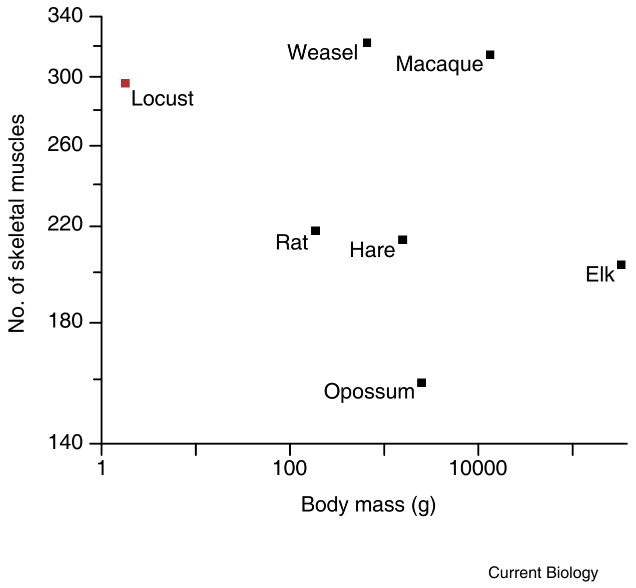


Figure 3. Insects and mammals possess similar numbers of muscles irrespective of body mass.

The number of muscles in mammals varies from 159 (opossum) to 322 (weasel). The migratory locust (*Locusta migratoria*) possesses 296 muscles. Data from [52,53].

vertebrate muscles suggests that the number of muscle fibres innervated by a single motor neuron is reduced and the number of motor neurons increased in muscles requiring more precise control [66]. Differences in the precision of movements between insects and vertebrates may arise from differing numbers of motor neurons, but this may also be a consequence of the biomechanics of the insect exoskeleton and the degrees of freedom of limb joints.

In conclusion, it is clear that the motor systems of insects are not necessarily inferior to those of mammals in ways that differences in brain size might suggest, with many size differences in motor control centres just related to the requirements of controlling bigger muscles. The differences in behavioural repertoire size between insects and large-brained vertebrates [48] are much less pronounced than one might expect from differences in brain size.

Cognition with Miniature Brains

While few would contend that insects can produce a large variety of behaviour routines with relatively small nervous systems, there is still a prevailing view that this is all there is — that insect behaviour is governed exclusively by such hard-wired routines, each triggered by a specific configuration of sensory input. Daniel Dennett, for example, points out the 'mindless mechanicity' of the digger wasp *Sphex ichneumoneus* that, by artificially disrupting its offspring provisioning procedure, can be tricked into performing the same complex routine over and over, even when this has become entirely meaningless [67]. While this is an intuitively appealing example to contrast the seemingly automatic behaviour of a small brained animal with that of humans, it creates a somewhat misleading image of insects as fully pre-programmed reflex machines. There has now been a century of work on insect learning behaviour. Much of the early work on insect learning focussed on simple associative processes, such as the memory for visual patterns, colours and places [68], and attempts to ascribe true cognitive abilities to insects were initially viewed with suspicion.

These doubts arose in part because some cognitive feats attributed to insects were clearly more a question of whether definitions of these abilities were sufficiently permissive to include insect behaviour, or whether experimental procedures were indeed comparable to those used on vertebrates. The last 15 years, however, have generated a wealth of literature from multiple independent laboratories on cognitive function in the insects, so that the existence of such abilities is no longer controversial. This includes work on attention-like processes in fruit flies and honeybees [69,70], categorization of visual stimuli (for example, symmetrical versus asymmetrical ones) by honeybees [7,71], contextual learning in various species of insects (for example, where a spatial position determines whether visual pattern A or B is correct) [24], sequence learning [20,25], various types of social learning in bees, crickets and flies [17,30], interval timing in bumblebees, where subjects must predict when a certain event will occur based on previous experience [72], associative recall, where a floral scent previously experienced by a honeybee in a certain place will trigger the memory for that place if the scent is experienced in a different location [73], and numerosity, where insects respond, for example, to the number of landmarks passed en route to a goal [74] (Box 2).

One particularly impressive ability displayed by honeybees is the learning of sameness–difference rules [27], where subjects are trained in a so-called delayed-matching-to-sample task. When learning the concept of sameness, honeybees are first shown a sample visual pattern A, then given a choice between A and B, where A is associated with a reward (Figure 4). Thus, bees need to memorise the first pattern and match one of the following pair to it. Moreover, bees can eventually learn a more general rule to 'choose the same ones' with entirely different sets of stimuli (for example, pattern C followed by C and D), even if they have not see these stimuli before. Perhaps even more impressively, they transfer the 'sameness rule' to visual stimuli even if it was entrained using olfactory stimuli. And finally, honeybees can learn the inverse concept: 'choose the different one', so subjects learnt to always choose the pattern that was *not* the sample — the 'odd one' [27]. While the mechanism by which bees solve this problem is not yet understood, these experiments and bees' performance are comparable to those performed on vertebrates [18], although *some* aspects of sameness/difference concepts might be considered uniquely human [75].

Although these feats are impressive, we should ask ourselves whether we are only surprised by them because we expect cognitive capacity to decrease with brain size, and a brain whose volume measures less than a millionth of a human's might appear unlikely to perform any complex operations at all. However, Srinivasan [76] has made the convincing point that rule learning, concept formation and categorisation might indeed be adaptive strategies *because* of, rather than despite, the miniaturisation of the insect brain. Thus, combining various objects to a single concept or category may be a strategy to economise on memory — memorising all relevant patterns by a common feature, rather than each of them individually. Perhaps wielding Occam's razor too extensively, Horridge [77] claimed that bees might actually extract only low-level cues — such as edge orientation, contour length or spectral content — from visual

Box 2

Learning processes in insects.

This is an overview only; there is no intention of completeness of phenomena, species, explanations or references — for each process we have chosen only one representative source and readers are encouraged to check the references in these papers. Note also that some of the phenomena are related or overlapping, for example the sameness/difference concept learning experiments were performed using a delayed matching-to-sample paradigm. Not included are basic, non-associative forms of learning (such as sensitization and habituation), or various forms of simple associative learning (such as excitatory and inhibitory conditioning, avoidance learning and so on), which are probably found in most animals. US – unconditioned stimulus.

Associative recall: Here, the triggering of route memory by exposure to a scent formerly paired with the target of the route; honeybees [73].

Attention: An ‘inner eye’ allowing the nervous system to ‘focus’ on limited aspects of incoming information; flies [69], honeybees [70].

Binding: The ‘tying together’ of features analysed separately in the visual system into a coherent image; bumblebees [78], honeybees [79].

Blocking: After stimulus A has been associated with a US, presenting a compound AB with US may not lead to conditioning of B; honeybees [68].

Category learning: Learning to identify different items as members of a class, for example ‘plants’, ‘chairs’, ‘dogs’; honeybees [71].

Concept of symmetry: Learning that any symmetrical (or asymmetrical) target is a member of a category; honeybees [7].

Concept of sameness/difference: Learning a rule to ‘always choose the same one’ or ‘always choose the odd one’; honeybees [27].

Context learning: Learning the appropriate response to a stimulus not via the stimulus itself, but by the context in which it occurs; cockroaches [119], fruit flies [91], honeybees [7].

Delayed matching to sample: Keeping a stimulus in working memory and match one from a set of options later; honeybees [27].

Generalisation: The tendency to respond similarly to stimuli that are similar to one that has previously been associated with a US; bumblebees [143], fruit flies [91], honeybees [68].

Interval timing: Learning to predict the timing of a future event from past experience with intervals between events; bumblebees [72].

Latent learning: Learning without rewards, for example in spatial exploration; ants [144], honeybees [68].

Motor learning: Learning movement patterns, as for example in flower handling techniques and wax comb construction in honeybees; bumblebees [108], butterflies [145], fruit flies [121].

Numerosity: Responding to the number of items in a display, not to size or other low-level cues; honeybees [74], beetles [146].

Negative patterning discrimination: Learning that two stimuli (A and B) are reinforced but the compound (A plus B) is not; honeybees [7].

Observational conditioning: A form of second order conditioning where one of the conditioned stimuli is the appearance of a conspecific animal; bumblebees [17].

Overshadowing: The inhibition of associating stimulus A with a US in the presence of another stimulus B; honeybees [68].

Overtraining reversal effect: If subjects are trained beyond saturation performance, they are more ready to reverse-learn; honeybees [68].

Pain relief learning: Learning to identify stimuli associated with the relief from pain as rewarding; fruit flies [147].

Peak shift: A bias away from an unrewarded option, arising from differential conditioning; bumblebees [148], honeybees [149].

Reversal learning: Learning that a previously correct option is now incorrect and vice versa; bumblebees [108], honeybees [68]; cockroaches [150].

Second order conditioning: Associating stimulus A with a US; if A is subsequently paired with new stimulus B, B will also be learnt as predictor of US; honeybees [68].

Sequence learning: For example, learning the sequence of landmarks leading to a food source; bumblebees [21], honeybees [20].

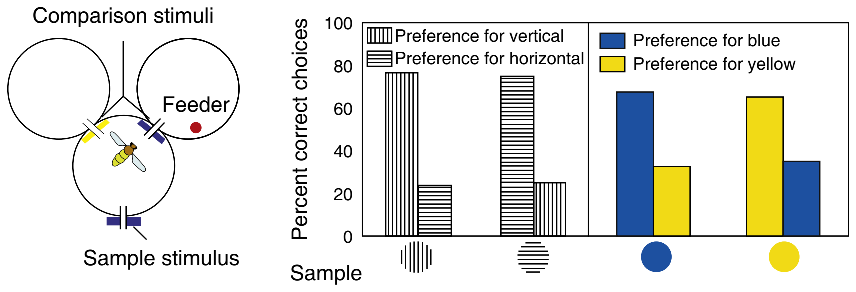
State-dependent learnt valuation: The phenomenon that perceived US strength depends on the internal state of animals, for example on hunger levels; locusts [151].

scenes, and never bind them together into a coherent image. It might, however, be very difficult to generate adaptive behaviour without such binding (compare Balint’s syndrome in humans), and indeed it has been shown unambiguously that bees can bind together various pattern features into an image [78,79].

The cognitive abilities of insects are less surprising if one considers the neuronal circuitry required to perform them. Artificial neural network analyses typically show that the minimum number of neurons necessary to perform a variety of cognitive tasks is exceedingly small (Figure 5). For example, a simple visual categorisation task (where patterns varying along a continuum are categorised by width or shape) can be solved with a network consisting of seven sensory neurons and five interneurons [80], and selective attention could be generated with nine sensory neurons and fewer than a dozen interneurons [81], plus motor neurons. In another set of networks loosely based on circuitry in insect mushroom bodies, it was shown that landmark learning, and indeed the active searching for novel spatial solutions, can be generated with very limited neuron numbers [82,83].

Basic numerical abilities (as found in bees [74]) have been simulated using a network of 50 visual input units (the ‘retina’), 450 neuron clusters generating a topographical map of object locations (normalising for location and size), and a set of 15 numerosity detectors that sum up the outputs from the location map [84]. Note that the units in this network are neuronal clusters, not individual neurons, but there is no *a priori* reason why such a network should not work with single neurons instead. Similarly simple networks can be used for sequence learning [85], as used, for example, in landmark navigation by bees [20,26], and path integration [86]. It is interesting to note that even more complex processes, such as route planning and anticipating the consequences of one’s own actions, at least at their most basic level, require neuron numbers that could still be accommodated in the insect nervous system [83,87].

Delayed matching-to-sample (DMTS)



Delayed non-matching-to-sample (DNMTS)

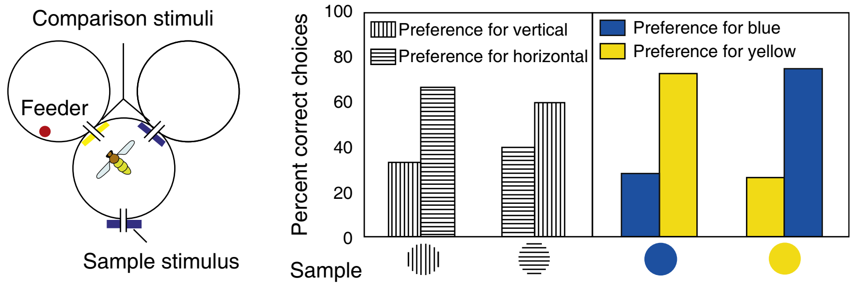


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Figure 4. Rule learning and the concept of sameness and difference in an insect, the honeybee.

Top row: Sameness rule learning: bees were trained in a delayed matching-to-sample paradigm, where they were first shown a sample of a visual stimulus (for example, yellow) when entering a Y-maze type setup. At the decision point, they were presented two stimuli (for example, yellow and blue), only one of which matched the one previously seen, and which marked the entrance to a chamber with a sucrose reward. After training, bees will not only be able to reliably pick the same stimulus as seen earlier, but will learn a rule to 'always pick the same one', no matter what the stimulus actually is, i.e. no matter whether it is yellow, blue, vertically striped, or horizontally striped. Bottom row: Difference rule learning (delayed non-matching-to-sample): in the same apparatus, bees can also learn to 'always pick the different one', so that they have to remember the sample stimulus, and then choose the stimulus that differs from it. Bees can even transfer these learnt rules from one sensory modality to another, for example from olfaction to vision. Redrawn from [27].

Are these artificial neuronal networks realistic, and likely to be similar to those really implemented in insect brains? In some cases, the answer might turn out to be 'no', but the important point is that some cognitive feats demonstrated in insects can, at least in principle, be solved with neuronal networks consisting of dozens or hundreds, not millions, of neurons. Insect brains, under stringent selective pressure to accommodate maximum computational power into minimal space, for many millions of generations, will certainly have had the possibility to arrive at solutions that are equally efficient as those discovered by neural network modellers. In the future, a better integration of the literature on minimal wiring solutions [48,88–90] and neural networks [80,81,83] with neurobiological work on learning and memory in insects [7,91] is desirable.

Menzel and Giurfa [7] have largely identified the neural circuitry involved in olfactory classical conditioning in honeybees, and have made the convincing argument that more cognitive forms of information processing could be achieved through modular organisation and lateral connections between modules, for example in the contextual learning of odours and visual stimuli [92]. As yet, we do not understand the full circuitry behind many cognitive abilities in animals, but it is clear that this is the desideratum, rather than the measurement of correlations between brain size and cognitive ability.

Neural Consequences of Changing Brain Volumes

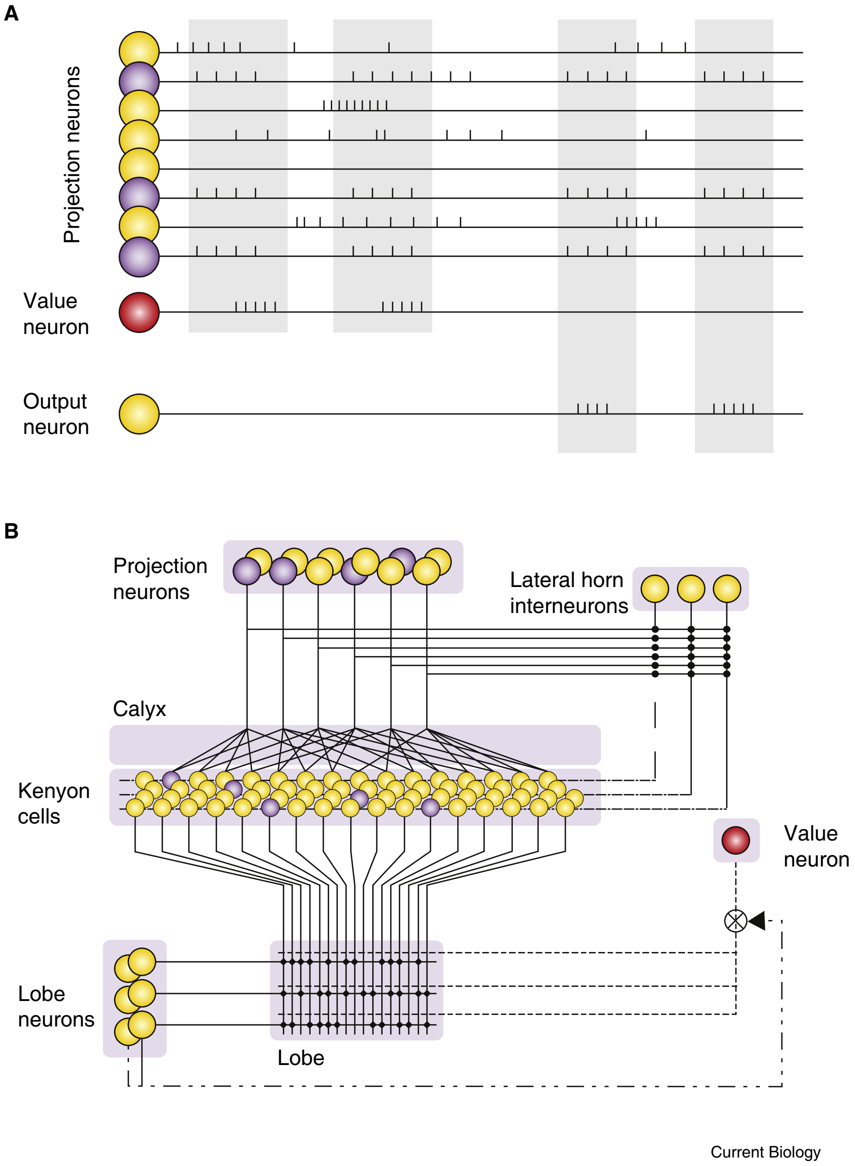
Comparison of closely related species shows that the absolute brain volume of both vertebrates and insects increases with body mass [10,93], although the relative brain volume decreases. Increases in total brain volume may be due to concerted changes throughout the brain or may be restricted to specific brain regions that expand relatively to the rest of the brain, in correspondence with ecological specialisation [41,94]. As we have discussed for sense organs, expansion cannot be entirely restricted to a specific region of the nervous system because information must be conveyed to and processed by neighbouring regions if the expansion is to affect behaviour [41].

As brain regions increase in size, so the distance that information must travel between regions increases. In vertebrates, the delays between regions can be substantial; even in small brains, delays can reach 100 milliseconds between hemispheres [95] and may be substantially longer in the smallest axons of the peripheral nervous system, which could have profound consequences for vertebrate behaviour. An increase in axon diameter increases conduction velocity, as does myelination [96]. Thus, as brains expand, so axon diameters and the proportions of myelinated axons must increase to reduce delays between regions [97]. Folding can reduce the distance between highly interconnected regions of the cortex and long-distance connections are sparse compared to short-distance connections [10]. Nevertheless, in mammalian cortex the volume of connections between distant brain regions (white matter) increases disproportionately faster than that of local processing (grey matter) [98].

An increase in the size of a brain region would increase the length of connections among neurons within that region and to other brain regions. As noted previously, longer connections increase conduction delays and energetic costs. Because of constraints on energy consumption and space, large numbers of long distance connections with high costs in terms of energy and space would be selected against. Instead, neurons make large numbers of local connections, only making relatively few long-distance connections [10,48]. Such a distribution of connections reduces connection lengths whilst still facilitating rapid dissemination of

Figure 5. Neural network model reproducing associative learning in the insect mushroom bodies.

(A) A simplified network in which the mushroom body is represented by the single Output Neuron that learns and later identifies salient patterns. During exposure to a stimulus conveyed by Projection Neurons the Value Neuron indicates the patterns to be learnt and later recalled. (B) An elaborated model of the mushroom body and the networks to which it connects. Input is provided by pairs of projection neurons that connect to single Kenyon cells, each of which is a coincidence detector spiking only in response to synchronised inputs from both pre-synaptic neurons. Learning of Kenyon cell activity patterns is instructed by a value neuron (carrying, for example, the sucrose reward signal; compare Figure 1); lobe synapses are strengthened in response to simultaneous activity in both the Kenyon cells and value neuron. Adapted from [118], with permission.



information throughout the brain. This pattern of connectivity promotes the proliferation of brain regions as brains increase in size, brain regions segregating to maintain a high level of local connectivity and reduce the number of long-distance connections. Novel brain regions and the circuits within them may be free to diversify, producing novel behaviours.

Insects lack myelin, though it is present in other arthropods [96], and increased conduction velocity is achieved solely through increased axon diameters. The largest axon diameters are achieved in interneurons with long range connections that form part of escape circuitry [60]. Although these interneurons will increase the volume of the ventral nerve cord, there are typically very few such neurons. For example, the desert locust, *Schistocerca gregaria*, has just four pairs of giant interneurons that transmit signals from cercal hairs for the initiation of an escape response. The fastest of these neurons have axon diameters of approximately 25 μm and conduction velocities of 3.9 m s^{-1} [60]. Thus, the small distances within insect nervous systems allow the majority of information to be transferred in interneurons with small axon diameters. Indeed, distances are sufficiently small within insect nervous systems that some interneuron populations transmit purely analogue signals, improving the efficiency of information processing further [41,99]. Transmission of analogue signals is restricted, due to their propagation and accumulation of noise, to short distances. Thus, within vertebrate nervous systems they are restricted to short sensory receptors and some visual interneurons [100].

Brain Size and Long-Term Memory Storage Capacity

There is no question that some vertebrates can store extremely large quantities of memories, with which insects presumably cannot compete. In a study famously entitled “Learning 10,000 Pictures”, Standing [101] concluded that human’s memory for pictures is virtually without limits. But it doesn’t require a brain that weighs more than 1 kg to store large quantities of information. Pigeons can remember about 800 images with substantially smaller brains, but the record among birds is held by Clark’s nutcracker, which is thought to remember the locations of several thousand seed caching places [18]. Within the food-storing birds like Clark’s nutcracker, there is evidence that storage capacity increases with hippocampus size [102,103].

There have been some attempts at determining memory storage capacity in social insects [104,105]. Typically, tests on insect memory capacity have come up with numbers in the single digits for any given set of items to be memorised, although it is quite possible that these are underestimates. The number of landmarks that can be stored by a honeybee is at least six, and bees can link these to specific routes that guide them to various food sources [106]. Honeybees form long-term memories of rewards to be expected at four

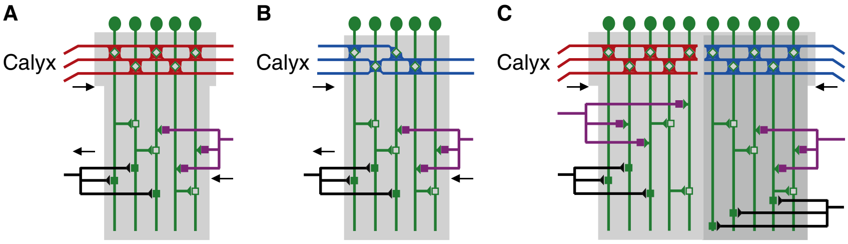


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Figure 6. The acquisition of novel pathways can produce novel behaviours.

(A) In basal insects the mushroom body calyces receive olfactory inputs (red). Parallel fibres receive inputs (purple) and make outputs (black). (B) In some insects (such as dragonflies) the olfactory inputs to the calyces have been replaced by inputs from the visual system (blue). (C) In hymenopterans (bees, wasps and ants) the calyces receive inputs from both olfactory (red) and visual (blue) inputs. (Adapted from [128] with permission from John Wiley & Sons, Inc.)

individual artificial flowers, but an upper limit has not yet been found [19]. Some (but not all) individual bumblebees (*Bombus terrestris*) can distinguish four rewarded stimuli from four unrewarded ones [104]. Bees can also link specific spatial (feeding site) memories to smells, but appear to be unable to form more than two such associations unless the feeders are further specified by distinct colours, in which case they can juggle three spatial position-smell-colour associations [92], albeit with less accuracy.

This appears to be a common theme: while insects appear to retain multiple associations in long-term memory, accuracy and task speed deteriorate as more information needs to be handled [107,108]. While tests of vertebrate and insect long-term memory storage capacity are not directly comparable, this capacity is probably lower in insects than in many large-brained vertebrates. It is also possible that there is more ‘adaptive redundancy’ in larger-brained animals, in that memories are written into multiple circuits to protect against interference or injury.

Likewise, there might be differences in working memory capacity and the amount of incoming information that can be processed in parallel by insects and some vertebrates [70]. Again, an increase of neural tissue here does not, by default, produce more types of neuronal operations or more advanced computations, just more storage capacity. However, searching a bigger library of stored information might enable an animal to generate more and better novel solutions to a problem, or find such solutions with higher probability.

Brain Size and Neural Information Processing

Changes in the sensory periphery alter the information extracted from the environment but changes in central regions can provide more processing power, allowing novel associations and computations. In addition to differences in the quantity of information that can be extracted, processed and stored by animals with different brain sizes, there is no question that there can also be differences in quality. For example, bees fail to solve transitive inference tasks [109] and it is unlikely that in the insects we will find instances of flexible tool use, insight learning, theory of mind, etc. Nonetheless, the remarkable work on cognition in corvids [110] shows that a brain that weighs about 10 g [18] can achieve many of the types of cognitive operation that great apes can, whose brains have a mass of several hundred grams [6]. This raises the question of whether absolute brain size plays any role at all in cognitive capacity — because both corvids and chimpanzees have similarly larger brains than expected for their body mass [110], they might have similar potential for intelligence [18]. The additional total brain volume found in primates might, to some extent, go towards processes unrelated to behavioural repertoire or cognitive capacity, such as we have described above.

Should we expect that an insect whose brain mass is similarly elevated above the regression line between body size and brain size as corvids or apes will be on a par with them in terms of cognitive capacity? Would we expect selection to produce *any* degree of cognitive capacity, entirely based on ecological demands, and independently of brain size? Probably not — one obvious reason is that neural circuitry cannot be infinitely miniaturised [111] and it is the actual circuitry required for any single task that is of more interest than the size of the tissue that contains the circuits. Artificial neural networks might provide working hypotheses as to the minimal neural substrate required for the types of higher cognitive functions found in birds but not insects, and whether some might indeed be too complex to be accommodated within the constraints of an insect head capsule.

In terms of absolute computational power, relative brain size provides little information. The number of computations within a given time that can be supported by neural tissue is dependent upon absolute brain size, the number and size of neurons, the number of connections among them and the metabolic rate of the tissue. The upper rate of action potentials that can be sustained is determined by the specific metabolic rate, which will be higher in smaller brains. Smaller brains can therefore maintain a higher density of computations. Thus, relatively large brains from animals with small body mass are likely to have higher specific metabolic rates than similar sized brains from larger animals. Hence, although the absolute numbers of neurons and connections primarily determine the computational power, the energy available for neural processing, which is affected by the specific metabolic rate, is also important.

When relating the size of a brain area to lifestyle and cognition, it is interesting to evaluate centres that are further away from the sensory periphery and known to be engaged in learning, such as the insect mushroom bodies [7,91]. Increases in the volume of central brain regions can occur through the replication of nearly identical circuits — most likely engaged in more parallel processing but not necessarily more types of neuronal computation — and the addition of entirely new circuitry, which may be most promising when searching for advances in cognitive ability (Figure 6). For example, the most basal extant insects, the Archaeognatha, have antennal lobes but lack mushroom bodies, which are important for discrimination of odours as well as learning and memory [35]. The mushroom bodies, like the mammalian cortex, are compartmentalised into distinct clusters (‘modules’) of Kenyon cells, and insects with larger mushroom bodies have more such subcompartments [112]. Intriguingly, scarab beetles that are generalist feeders not only have larger mushroom bodies with more sub-compartments than more specialised species, but there is also a suggestion of differences in innervation patterns of the mushroom bodies depending on feeding ecology: generalists, but not specialists, might receive direct input from the optical lobes (not just chemosensory inputs as in most insects), possibly facilitating the kind of cross-modal cognitive operations that Srinivasan [73] has described for honeybees, and for which, at least in flies, the mushroom bodies are essential [91]. Such cross-connections between specialised modules are often critical for the acquisition of novel cognitive functions: for example, in humans there are direct projections from the neocortex to the major vocal motor neuron groups, which are either absent or weaker in non-human primates [113].

Returning to our comparison of the insect and vertebrate visual systems, it is clear that vertebrate visual systems contain greater numbers of distinct central visual areas specialised for a variety of tasks. For example, the vertebrate dorsal and ventral visual pathways contain numerous brain areas containing highly specific receptive fields and are involved in parallel and serial processing of visual information. Although neurons in insect visual systems possess receptive fields similar to those found in mammalian V1, no equivalents of the receptive fields found in higher visual centres, such as those in the dorsal and ventral visual pathways, are known in insects. These pathways involve numerous additional serial processing stages that allow the computation of novel receptive fields, for example neurons in the human ventral visual pathway that respond to individual faces [114].

Serial and parallel processing are essential for computing novel receptive fields and generating computational maps. Parallel neural pathways allow sensory inputs to be processed in different ways to extract information. Such processing can allow the computation of variables not directly represented in sensory inputs, such as the computational map of auditory space in the midbrain of barn owls [115]. Within large brains, additional parallel processing pathways and stages of serial processing allowing the computation of novel receptive fields may be added more easily than in insect brains where space may impose more severe constraints. Insect brains also contain neurons that respond to variables that must be computed from sensory inputs, such as interneurons in the anterior optic tubercle of locusts that encode the solar azimuth by combining information about the polarization pattern of the sky with spectral and intensity gradients [116]. However, in insects, neurons representing variables computed by combining multiple sources of sensory information appear to be present in smaller numbers than in vertebrates.

In honeybees, foraging experience induces an expansion of the mushroom bodies beyond the growth that would otherwise occur without foraging experience [117]. As there is no adult neurogenesis in bees, this increase is caused by enhanced dendritic outgrowth and branching of the ~170,000 Kenyon cells in each mushroom body [117]. Associative learning in the mushroom bodies can be realistically modelled with networks comprising only a few hundred neurons [118] (Figure 5) — a tiny fraction of those actually present that could not easily explain the volume changes that are actually observed. In some insects, additional cognitive functions, such as context learning and generalisation, also occur in the mushroom bodies [91,119]. While the volume changes in mushroom bodies with experience are intriguing, there is little information on the functional consequences of these changes. Although there is an attraction to 'small' nervous systems with 'simple' processing, a structure containing 170,000 neurons presents a formidable challenge to any comprehensive understanding of internal function even with multielectrode recording techniques.

In recent years, several studies on vertebrates have found a correlation between brain size and some form of learning flexibility, including the generation of novel 'innovative' responses to environmental challenges [13,120]. Again, the neural circuitry involved in such innovation, and whether insect brains are prohibitively small to contain such circuitry is unclear. Whether insects can compute novel solutions to spatial problems based on previously learnt information (acquired in separate learning trials) is controversial [23]; again, however, it is interesting to point out that neural network analyses indicate that the generation of such novel solutions is neither computationally demanding nor does it require large neuron numbers [83]. Can insects 'invent' new behaviour patterns? There has been no systematic study — obviously the observation of novel behaviours requires confronting the subjects with unconventional challenges. In one paper entitled "Can a fly ride a bicycle?" [121], fruit flies were reported to solve motor problems that no insect had ever encountered in evolutionary history before.

In another experiment, all foraging bumblebees returning from a foraging bout were caught in black film canisters to weigh them [122]. All bees initially tried to avoid capture; their natural response is phototaxis and escape from dark places when threatened. Some bees reacted with overt aggression. Eventually, however, some individuals learnt to land voluntarily in the canisters, effectively using them as a means of transportation into the hive – occasionally, even if canisters were held in the air several meters away from the nest by the experimenter. One might counter that this reflects simple associative learning of the appearance of the container with being released into the nest — but it is not trivial, firstly because there was often a substantial delay between capture and release, and secondly because this behaviour required the complete suppression of the instinctive escape responses that normally operate during capture. In a sense, therefore, the observed behaviour is no different from the reports of pigeons cleverly using London Underground trains [18]. Because larger brains can extract and store more (and more detailed) information, having larger memory storage facilitates the generation of novel solutions based on previously stored information. In addition, neuronal connections between modules (brain areas) that process and store different items and types of information will enable the generation of new behavioural solutions with higher probability.

Conclusions

The search for correlations between overall brain sizes, cognition and aspects of animals' natural history is riddled with complications [12], and our knowledge of insects' often impressive behavioural repertoire size and cognitive ability adds to these difficulties. A high proportion of differences in brain volume, especially between species of different sizes, will be related to the fact that these animals support larger sense organs and their need to move larger bodies [10]. Bigger sense organs necessitate larger amounts of neural tissue to evaluate the information, providing more sensitivity and detail, but not necessarily higher 'intelligence'.

It is now clear that miniature brains can achieve many more types of cognitive operation than was assumed 15 years ago, but perhaps we should move away from just marvelling at the 'intelligence' that can be generated by smaller-than-human brains, despite the public interest garnered by such findings. Given that artificial neural networks required for many complex cognitive tasks require relatively few neurons, we might instead be surprised that many animals have such big brains. There might be relatively little mileage, for example, to hunt for intraspecific correlations between brain size and associative learning ability in insects (or larger animals), when even the smallest nervous systems, such as that of the nematode *Caenorhabditis elegans* with its 302 neurons, are capable of associative learning [123]. Even if such correlations should be statistically significant, they are likely epiphenomena of other processes, for example differences in sensory performance. Despite the obvious ability of larger animals to transport and feed larger brains, they should be under selective pressure to minimise expensive neural tissue that isn't needed. It is thus clear that we need to understand the neural circuitry behind a given cognitive ability better, and in the absence of neurobiological tools to monitor extensive circuits' activity with sufficient temporal resolution, artificial neural network analyses should be helpful to formalise what's minimally needed.

Almost all of the molecular components of neurons — ion channels, neurotransmitters, pumps, exchangers and G-protein receptors — are present in both vertebrates and insects, and thus, presumably in their common ancestor. Moreover, connections between neurons show similar plasticity to those found in vertebrates, including short-term, spike-timing-dependent and long-term plasticity [124,125]. Neural circuits perform similar computations in insects, including lateral inhibition, feedforward and feedback excitation/inhibition and presynaptic inhibition [60,126,127].

Thus, rather than an explanation based on the evolution of a novel molecular component or greater numbers of neurons, we argue that new neurons recruited into novel pathways and novel brain regions resulting in greater serial and parallel processing of information and links between processing pathways are more likely to contribute more to qualitative changes in behavioural performance. To the extent that developing nervous systems are pre-programmed to extract regularities from the environment by self-organisation, basic forms of cognition will 'pop out' even of relatively small neuronal circuits. Ultimately, we will understand brain evolution better if we appreciate that cognitive performance can arise early on and in small nervous systems, or relatively easily by convergence based on environmental challenges, using the same self-organising principles. Larger brains in animals with larger carrying capacity facilitate, but do not necessarily automatically generate, the segregation, conversion and addition of more (and more specialised) modules that might ultimately be used for novel cognitive functions.

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