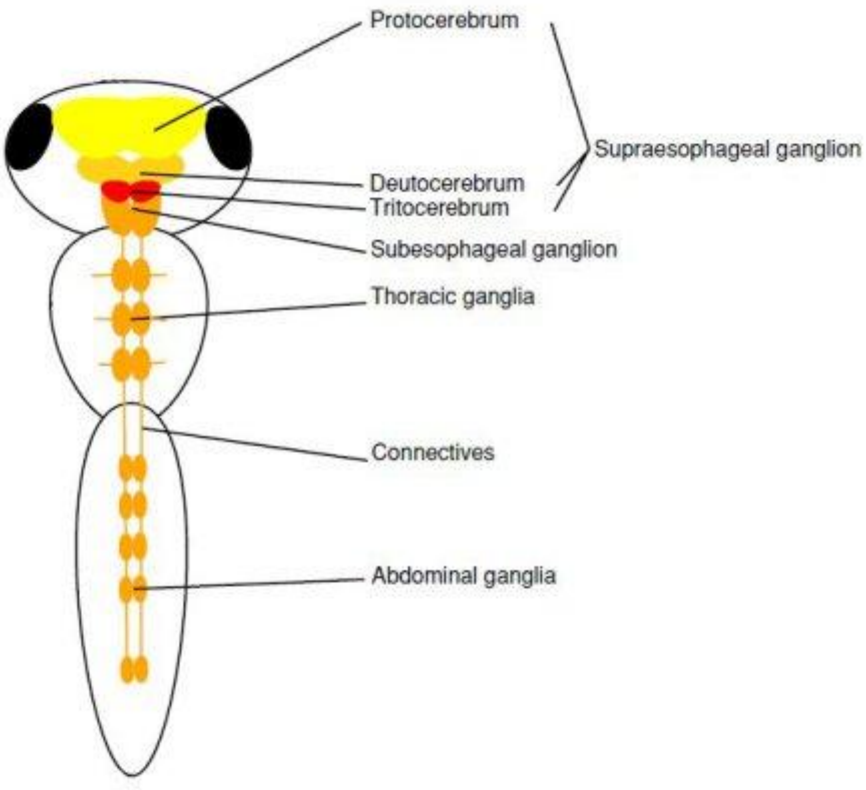
INSECT BRAINS AND ANIMAL INTELLIGENCE

One of Linnaeus's criteria for erecting his Insecta group was that they had no brain. It's not hard to see why he would classify them like that. Decapitated insects will still execute the same behaviour. Buffon, one of the great naturalists of the eighteenth century, wrote that "the hippobosca, equina, or horsefly, will live, run, nay, even copulate, after being deprived of its head." *Drosophila* flies live for several days completely normally without a head: they will fly, walk and copulate (okay, they have to be raped since a headless female won't start courting rituals). Mantids, however, do start their mating dance when beheaded. Long-term memory in cockroaches will stay even when the head is removed. It seems amazing at first, but it's really quite clear how this all works when you look at an insect's central nervous system (CNS).

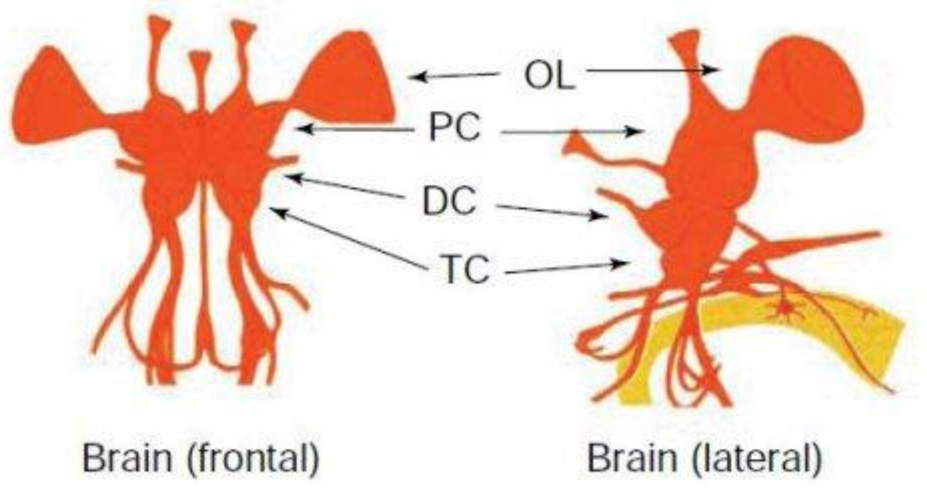


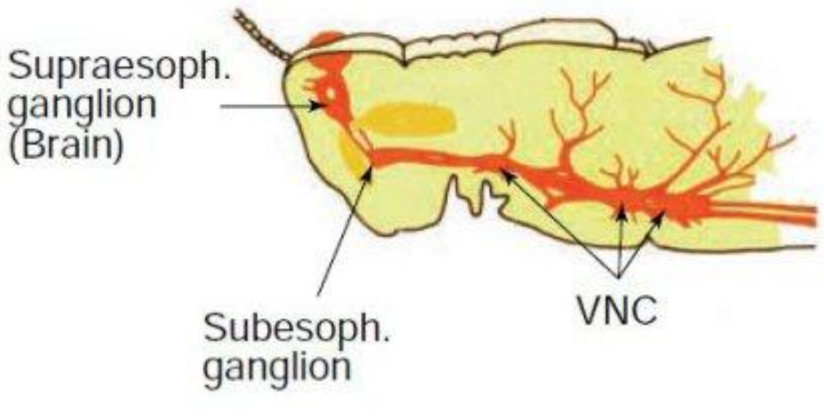
Ground plan of an insect's CNS

The brain of any animal is part of its CNS. Vertebrates have a brain comprised of many regions in the head, and a dorsal nerve cord running down the body in the spine. The insect CNS is somewhat different: the nerve cord is ventral with a ganglion in each segment of the body. The head contains two ganglia: a **supraesophagal** and a**subesophagal** ganglion. When referring to the insect brain, we usually mean the supraesophagal ganglion (also called the anterior brain;

from now on, just brain). Just as background, ganglia are bundles of neurons packed together.

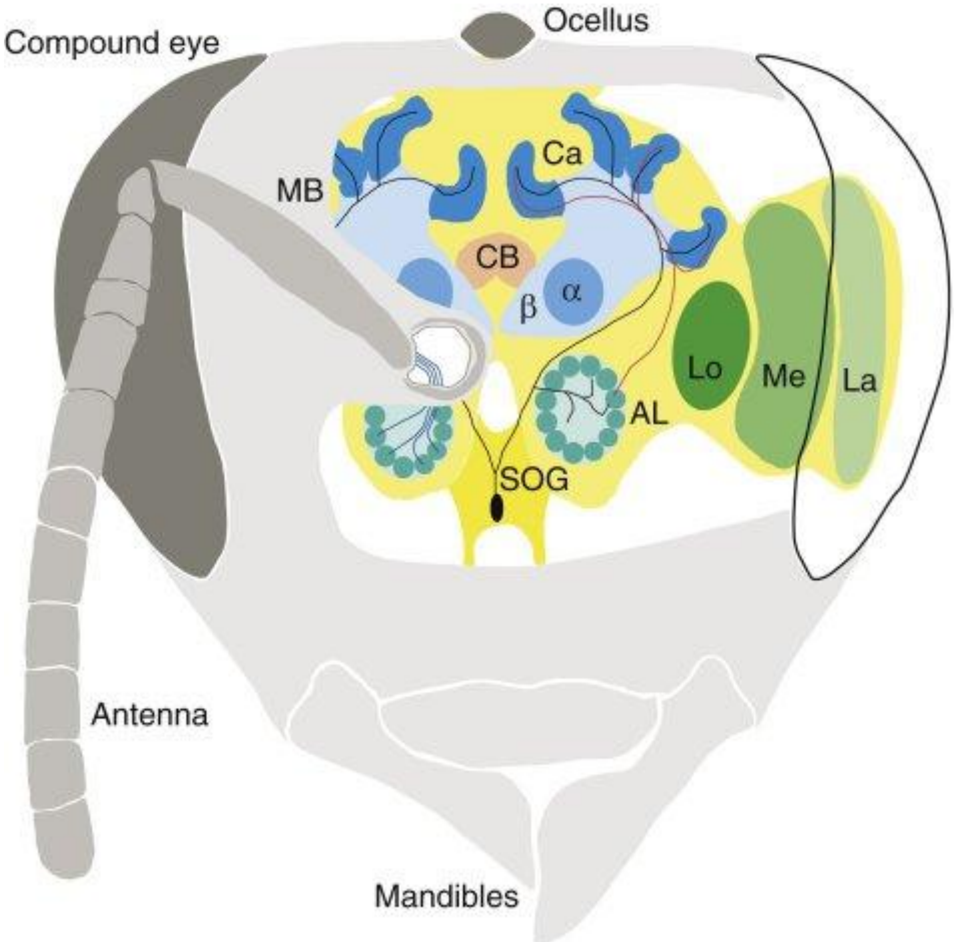
Of course, it should always be kept in mind that the insects are the most diverse group of animals, and this is also seen in their CNS arrangements and in their brain structures. The brains of insects are exceptionally malleable, and they can vary even within species (this is best seen in eusocial insects like ants or bees, where members of different castes have different-looking brains). Nevertheless, they are all variations of the same ground plan.





The brain is made up of three regions: the **protocerebrum** (PC),**deuterocerebrum** (DC) and **tritocerebrum** (TC). The PC is by far the largest region and contains the **mushroom bodies**, the **pars intercerebralis**, the **central complex** and the **lateral accessory lobes**. Two very prominent **optical lobes** are present, and they are responsible for processing the inputs from the eyes. They are attached to the PC, but they're not part of it. The DC contains the **antennal lobes**, which process the information coming from the antennae. The TC is the smallest part of the brain, and is also the least studied – it may have a function in tasting food. The total number of neurons varies with each insect, but *Drosophila* has around 100000, while a regular honey bee has ~1000000.

Let's look at what are frequently called the "higher" brain centers: the mushroom bodies and the central complex in the PC.



Frontal section of a bee's head. MB: mushroom body; Ca: calice; alpha, beta lobes; AL: antennal lobe; SOG: suboesophagal ganglion.

The mushroom bodies are a pair of **neuropils** (bunch of neurons). In the honeybee, there are ~340000 neurons in them – making up a significant portion of the bee brain. They're made up of three regions: the **calices** (Ca), the **peduncle** and the **alpha and beta lobes**. The structural organisation of the neuronal cells in the mushroom bodies is unique (in fact, they're given their own name: **Kenyon cells**). The calices serve as the input areas, the peduncle is the 'transfer region' and the lobes are the output region.

In most insect species, the mushroom bodies primarily recieve olfactory inputs: Odourant information is relayed from the olfactory receptors, through the antennal lobes and into the calices. In the case of cockroaches and locusts, tactile (touch) and gustatory (taste) inputs are also found. Bees and wasps, which are predominantly visual insects, have two exceptionally large optical lobes connected to the calyces.

The diversity of insect brains is most apparent in the mushroom bodies, since they are often compartmentalised, with each compartment dedicated to each input. The functional output of mushroom bodies is still a matter of debate. They are mostly involved in sorting out information from the different sensory inputs, since there is little evidence of any direct downstream connection to other brain areas. They may be involved in pattern recognition, as in locusts, where specific Kenyon cells activate depending on specific smells.

But the coolest function they have is in learning. It's no secret that insects are smart and have considerable memorisation ability. Manipulating the mushroom bodies (not allowing them to develop properly) has always resulted in loss of short- and long-term memory. There is a strong correlation between mushroom body size and memory in hymenopterans (bees, wasps, ants) as well as between size of the mushroom bodies and behavioural complexity. The reason for this is the Kenyon cells' remarkable plasticity, in that they will readily rebuild the neural fibers, acting as a sort of neural substrate on which new memories can grow.

In contrast to the mushroom bodies, we don't know that much about the central complex. It forms a line in the middle of the brain, and is made up of four interconnected regions: the protocerebral bridge, the center body (which has a lower and upper part), and the noduli. It's connected to almost all other PC regions, with the noteable exception of the mushroom bodies.

In locusts and bees, the compound eyes directly connect to the protocerebral bridge. The ocelli are also innervated by the central complex, and there seems to be a strong connection to the pathway responsible for polarised vision. That said, blind insects also have strongly developed central complexes, so they must have some other role.

In locusts, it's connected to the ventral cord, suggesting a role in movement. This is an interesting proposition, given that it's right between the left and right hemispheres of the brain, and it's further supported by the fact that those insects that can perform complex, asymmetrical leg movements (like weaving silk threads) have highly-developed central complexes.

There is also the possibility of the central complex playing a vital role in behaviour, since neural activity there is always correlated with the expression of specific behaviours. For example, changes in activity levels are seen at the start and end of flight in locusts. This is not limited to just walking and flying, but also includes visual searches.

The most definite proof comes when central complex development is suppressed. In *Drosophila*, this leads to inability to fly and strange walking, indicating that while it is not necessary for initiating leg movement, it is needed for control. If only the central part of the central complex is disrupted, the fly has difficulty orienting itself and cannot deal with asymmetries: they can't fly in a straight line, for example.
Combined with their likely role in the visual system, there is also a chance that they are integral for insects to calculate their travel paths, especially in migrating insects like the locust. Locusts have a very well-developed polarised light detection system. They see polarised light in the sky and use it as a compass to guide them on their journey.

The subesophagal ganglion (also called the posterior brain) is made up of three fused segments and is responsible for controlling the mouthparts (mandibles, maxillae and labium), and has a dorsal lobe for connecting the anterior brain to the rest of the CNS.

The thoracic ganglia are not only responsible for controlling the appendages (wings, legs, etc.) but also collect information from the environment (wind strength, sound), and relay these back to the brain.

This is a decentralised system: the brain doesn't control everything in an insect. Mating and moving are jobs for the body's ventral nerve cord, and the ganglia can store information. This explains the examples I mentioned at the start.

One of the most painfully idiotic myths surrounding insects is that their behaviour is limited, compared to animals of "higher intelligence". This is not true. Insects have many sensory inputs: their antennae let them feel and smell; they have hundreds of eyes; their body is covered in hair that lets them feel the wind. All these inputs come together and the insect has to decide what it will do. If they move and the smell of food gets weaker, they change direction. They regulate their wings' flapping depending on the wind speed. They will learn where there is a plentiful source of food and they will learn how best to capture that specific type of prey. These are not predetermined behaviours, they are learned from experience.

Ants can travel very long distances in search of food, but still come back to their nests. They do this by counting their steps and by memorising landmarks. Some insects will fly over landscapes taking mental snapshots of where they are so they can find their way back. Bees can recognise specific patterns, which helps in reminding them which flowers are cool or for recognising predators. Insects can manipulate their environment and make tools, as anyone who has observed ants can see.

But detractors will say that their behaviour is predictable (as if that's an indication of animal cognition!) It's true that insect behaviour can be seen as being hard-wired: pheromone-induced behaviour is a prime example of an insect going through predetermined steps. Escape mechanisms are another one: blow on an insect's wind-flow detectors (this is most amusingly done with cockroaches by blowing on their cerci) and it will have a reflex reaction similar to what happens when you put your hand on a hot plate: you don't think, your hand just moves away by itself.

But looking at insect behavior like this is deceptive, because the very same can be said of any other animal, even us amazing humans </sarcasm>. It's a drastic simplification and belies the complexity of insect behaviour. Insects fly and have to stabilise their vision so that they know where they're going. This is also an automatic action, just like your eyes automatically focus depending on how far you're looking. But the amount of information that goes into gaze-stabilisation is enormous, and it comes from multiple sources: the compound eyes detect vision; the ocelli detect light intensity; the halteres detect the body's position; hairs detect the wind speed. All this goes through the relatively tiny nervous system of the fly and the brain adjusts the head.

And even so, not all insect behaviour is just like letting a program run. Honeybees have an elaborate dance language, and no two dances are the same: the dance depends on distance and orientation, and changes dynamically.

The problem most people have with insect behaviour is that it's very polarising. On the one hand, there is the characteristic very inflexible, hard-wired behaviour we all know of, but there is also the startling ability to learn. Damselflies will always fly upside down when the light comes from below, but they will flawlessly fly through a complex maze and memorise its layout.

Let's look at true sociality, which is a purely entomological innovation (among the vertebrates, only naked mole rats are eusocial; humans don't come close.) Not only is it an example of insect intelligence (recognising and learning from nestmates), but look at the elaborate architecture of a hornet nest, the climate control in a termite colony, the symbolic communication in bees, the chemical communication systems in wasps, ants making slaves, farming and waging wars. All these are achieved with less than a million neurons.

This brings us to the concept of intelligence. What can be used as an indicator of intelligence? Whale brains weigh 9 kg and have over 200 billion neurons. Human brains weigh between 1 and 1.5 kg, with around 80 billion neurons. A honeybee brain is 1 mm^3 and has less than a million neurons. Brain size, therefore, is not a good predictor of intelligence, if it's measured by behavioural repertoire, innovativeness or sociality. In any of those examples, a honeybee will come out as more intelligent than a human or a whale.

How about learning speed? Again, a bee will beat out a human (and any other vertebrate), even when the life spans are equalised. This is an example of how difficult it is to quantify intelligence. I'm not saying bees are the most intelligent animals, but if you reduce it down to a mere statistic, they will come out on top simply because of the radically different nature of the brains in vertebrates and insects.

There is no unique feature of vertebrate intelligence that isn't found in insects. Vertebrates can memorise places, insects can too. Both have a sense of time. Both can call on past experience to make future judgements (as in: I came here at 3 oclock yesterday and ate a delicious aphid. I'll do it again today!) Learning rules? No problem! Categorising and sorting out information? Again, found in both groups. Even Pavlov's dog experiment, which has traditionally been cited as a vertebrate-only type of response (salivating in expectation of food), has been replicated in a cockroach. It seems there isn't much that vertebrates, with their relatively enormous brains, can do that insects can't. Why?

Having a large brain does not add any capabilities, it just improves the resolution. Think of a computer: you can have a a dual core CPU, but it won't bring you much if you're only running Windows 98 and Minesweeper on it. Complexity is not a matter of power (i.e. number of neurons), but the ability to do more things. In terms of behaviour, a honeybee is in a completely respectable position, according to how ethologists classify behaviour. Insects range from between 15 to 59 (the number rising with level of sociality). Dolphins have 123.

The honeybee scores 59: that means it is capable of 59 distinct behaviours, including building specifically-shaped honeycombs, manipulating pollen to stick them on their body, various dances as a means of communication, decieving its enemies in active combat, cleaning the nest and even warming its fellow nestmates by shivering (sharing body heat). A large mammal has a brain size that's a million times larger than a bee's. Yet they can only do two to three times more of the same kinds of behaviour. Not quite what one would expect, even if we accept the limitation of such ethograms.

What about memory? Humans can store a virtually unlimited amount of pictures, which is not that impressive, considering that birds with much smaller brains can memorise the locations of thousands of food stores. There aren't any studies that have determined an upper limit for insect long-term memory. Bees can memorise at least six locations, and three paths leading to each. They can remember at least four good choices and four bad choices. These memories are not just visual; they can also remember them by smell, and the overall memory is often a mixture of smell, location and colour. Of course, considering that memory capacity is directly linked to brain size (more neural substrate), we cannot directly compare insect and vertebrate memory capacity.

Is it really so surprising that insects have such advanced cognitive capabilities? No. A brain with a volume less than a millionth the size of a human's might seem unable to perform complex operations (because of that horrible generalisation the vertebrate people have been putting out about relative brain size and cognition). In fact, insect cognition is so advanced **because** of the brain's miniaturisation, not despite of it. They do not collect information by quantity, but by quality (in the visual system's case, a greater range of light frequencies and all sorts of edge-detection and pattern recognition systems, but at the price of resolution and clarity). This requires less neurons, but gives much more flexibility and information.

This, however, is not as advantageous as it seems. It's unlikely that we will find insects that have flexible tool use, that are insightful or that have some sort of theory of the mind. Then again, the 10 g brain of a corvid bird can achieve the same types of cognition of a great ape. Again, this speaks against the whole relative brain size as a measure for intelligence. But it's important not to get too extreme in dismissing that notion. Expecting selection to produce any desirable degree of cognitive capacity independent of brain size, and dependent only on ecological factors, is a silly mindset. What I've been trying to say through this section is that it's not the size of the tissue that matters, it's the type of circuitry – and this circuitry cannot be miniaturised to an unlimited degree.

Now let's go back to the mushroom bodies, since they seem to be most implicated in the effect of lifestyle on cognition and learning. Like the mammalian cortex, the mushroom bodies are compartmentalised into modules; the larger the mushroom body, the more modules there are. And here we can make an interesting observation. Scarab beetles, which are generalists, have larger mushroom bodies with more compartments than even honeybees and flies (who are more specialised in their ecology). More compartments mean more chances of new interconnections, and therefore new cognitive abilities – and this is directly related to the scarabs' ecology. A similar effect can be seen in humans, comparing them to other primates: our neocortex has developed connections to the motor neurons that control the vocal machinery, and this is what leads to language (our major cognitive innovation). Non-human primates do not have this neural connection.

And this leads to a realisation that every biologist interested in this field has to understand, and one that I've brought up several times. Correlating overall brain size and cognition is pointless, since an increase in brain size is simply an increase in processing power needed for supporting a larger organism. It will not lead to higher intelligence. A Caenorhabditis elegans worm, with its 302 neurons, is capable of learning. This is not a marvelous fact – it's to be expected. The real surprise comes from the fact that so many animals have such large brains! All the basic components of neurons are present in vertebrates and insects, and are probably shared from their last common ancestor. Cognitive ability does not come from new types of neurons, or just more neurons. It is new links between different bundles of neurons that lead to tangible changes in behaviour: to understand the brain, we don't look at the size of it, but at how its different components interact.

And as many of you have wondered why I have such an insect brain fetish, but I didn't really explain it in the post, here's an elegant quote.

"***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 marvelous atoms of matter in the world, perhaps more so than the brain of man.***"

Charles Darwin, 1871.