Chapter 25

Overview

It's possible to detect a simple theme underlying the complexities of brain evolution. What brains do is discover correlations. Neurons which record different sorts of event, or different aspects of the same event, put their information together, usually by converging on another neuron. The more layers of neurons there are through which to sift the sensory input, the greater the amount of information extracted. And the larger the number of processing channels the greater the potential number of interconnections, and thus of cross-correlations. Bigger brains make more correlations. As a result the actions they direct can be more effectively fitted to the details of the environment. The larger the brain the more efficient its possessor can be about acquiring energy and the choosier about how it's spent. The neocortex, as it expanded, offered more and more potential for this. And in humans - thanks largely, no doubt, to that area at the very front of the frontal lobe - the capacity for making correlations has been taken to an extreme, and has created the potential for abstract reasoning.

Detecting coincidences and making correlations is not by any means unique to brains. It can be achieved elsewhere, as when *Aplysia*, after being buffeted a few times on the tail and then on the siphon, learns to withdraw its more vulnerable parts after the first prod, without waiting for further insult, thanks to a connection from tactile neurons in the tail to neurons in the siphon and gill. An arrangement like this offers limited scope for expansion, however. Brains, where information from many sources is reported within a limited compass, provide vastly more scope both for making connections between sensory inputs and for applying the results.

The most extravagant example so far discovered of multiple correlations within a single sensory channel is provided by the primate visual system. Preliminary rounds of processing in the retina and the lateral geniculate nucleus of the thalamus reveal small areas of contrast. This data is transmitted to the neocortex where inputs from adjacent retinal areas are compared to reveal lines, edges and corners. Inputs from receptors sensitive to different wavelengths are processed through several episodes of correlation to create umpteen shades of colour. Inputs from the two eyes are compared to establish distances. The conclusions about edges, textures, their relative distances and the colours attached to them are then put together to reach a decision about the nature of the visual object or scene. This decision is a prediction about the potential implications of the object or scene for other sensory channels, and about whether there is a need for action - a prediction that can be made because of the intersensory correlations that have been recorded in the past.

At the same time neurons in the parietal cortex are correlating what the visual receptors register with the direction of gaze and the position of the head, and establishing just where the stimulus pattern is in relation to the body, in case a motor response is necessary.

Higher cognitive powers also depend on neurons which make correlations. Mirror neurons, responding both to actions performed by the self and those performed by others, are particularly notable examples. Combining the activity of the mirror neurons with the evidence of the distance senses and with interoceptive feedback - the feel of performing a movement - allows the actions of the self to be distinguished from the actions of others. The ability to relate the actions of others to those of the self while nevertheless distinguishing between the two contributes a vital element to the development of a concept of self. It incidentally provides the means of working out that the figure gesticulating in the mirror is a reflection of the self - something that only larger brains achieve.

There are also emotional mirror neurons. Some cells in somatosensory cortex fire not only in response to painful input but also at the sight of someone else in similar pain. Neurons in the insula, through which so much information flows to prefrontal cortex, respond to pain, disgust and various other emotions when they are exhibited by others, as well as when they are experienced by the self. The correlations effected by these emotional mirror neurons can be supposed to be what makes emotions infectious, and creates the possibility of learning by sharing the reactions of others. They

have contributed enormously to the benefits reaped from prolonged maternal care, and from living in social groups.

Much imitational and emotional learning, meanwhile, is facilitated by what might be called attentional mirror neurons, found in the parietal cortex, which fire both when an animal's gaze is pointed in a certain direction, and when another animal is observed to be looking towards that point in space.

The various mirror neurons supply a foundation for the idea of others as entities similar to the self, with similar reactions and motivations, a talent which provides the means of predicting the likely behaviour of a conspecific.   A well-developed concept of others as similar entities to the self, acting and reacting in more or less similar ways, opens the way towards the invention of language.   This clearly depends on being able to compare the sounds produced by the self with those made by others. It also requires relating the action of producing a word not only to the sound produced, but also to its reference.   Full language becomes possible when the words can be put together in meaningful relationships.   Abstract thought becomes possible when there are sufficient layers of neuronal processing to put several material concepts together and find an underlying theme.

However, the correlations most vital for survival are of course the most basic ones - those between events in the outside world and effects on the organism; in other words, between reports from distance or boundary senses and reports from boundary or internal senses.   It's only when connections exist that can turn data about the self into feedback about the results of acting on sensory patterns in the external world, and use that feedback to modify future behaviour, that it becomes worthwhile to collect more data about the external world, in addition to that which drives hardwired responses.   On the other hand, where there is a potential for 'reinforcement' of a behaviour almost any addition to the capacity for collecting sensory data about relevant events, and for winnowing information out of it, becomes worthwhile.

Machinery for turning inputs to the boundary and internal senses into feedback was well established long before the neocortex appeared.   It was clearly accompanied by some very effective sensory processing, even if there was nothing like the elaborate neocortical correlations.   All this provided a solid foundation, on which the neocortex could be built.

In the vertebrate brain four particularly important areas have been identified where links are forged which turn one sort of sensory input into feedback about the significance of another.   They are areas where synapses can be strengthened by use, or weakened by sparse employment, a process that constitutes learning.   All four are found in almost all vertebrates.   Together these four pieces of neuronal machinery clearly contributed enormously to the survival of their owners in a competitive world.   Probably they constitute important reasons why a vast number of less complex vertebrates and non-vertebrate chordates failed to survive, leaving an enormous gap today between the few remaining non-vertebrate chordates and the least complicated of the vertebrates.

The basal ganglia

If the basal ganglia have their origins in arrangements for steering, slowing and stopping, as seems likely, they must date back to the very beginnings of locomotion, or indeed earlier, since the means of reorientation probably evolved before locomotion did.   The first elements of the circuitry must have been part of the conglomeration of neurons which grew at the front of ancestral bilateral animals long before there was anything that could qualify as a brain.   The original components functioned, I've suggested, to inhibit contractions on one or both sides of the body, thus producing turns or decelerations.   Possibly the transmitter in the very early stages was dopamine, operating on inhibitory, metabotropic receptors to fairly gentle effect.   This would be adequate in a primitive, slow-moving creature which needed only to immerse itself in the richest distribution of food particles, rather than to aim for a specific target.

As both muscles and sensory systems grew more efficient more delicate controls would be beneficial, with faster signals, conveyed by neurotransmitters rather than a modulator.   And a

feedback connection evolved, along with some synaptic plasticity, creating an ability to correlate variations on the innately determined stimulus patterns that attracted an approach with what was gained, and to find that some versions didn't repay the effort. This development seems likely to have involved the evolution of the neurons that inhibit the inhibition, and perhaps a new application for dopamine.

Initially the stimuli amongst which discriminations were learnt were probably defined by new methods of combining the sort of sensory data already being acquired. However, the ability for this sort of learning meant that it became useful to collect additional sensory data if it helped to identify stimulus patterns worth approaching, so all sorts of improvements to distance senses would become worthwhile.

Meanwhile the chain of neurons controlling locomotion grew longer and more complex, as bilateral fins, jaws and other new accessories appeared, and the contractions of all the various muscles had to be co-ordinated. The need for well-timed inhibitions became even greater, and new feedback connections must also have emerged.

Muscles to rotate the eyeball probably appeared even earlier than fins, judging by the fact that lampreys are equipped with them. The direction of the gaze must of course be correlated with the orientation of the body if there is to be action on a visual object, so the machinery that organised bodily orientation and the direction of travel was extended to cover eye movements as well.

The deployments of skeletal muscle which constitute genetically determined responses to genetically determined stimulus patterns must be managed by the basal ganglia, with the stimulus patterns identified in the midbrain or the thalamus. Much of the straighforward sort of learning which defines the genetically determined stimulus pattern rather more closely - the sort that can be defined as conditioned learning - also depends on the basal ganglia. These hardwired and conditioned responses must guide the development of sensory and association cortex, ensuring that its sophisticated processing abilities are applied where they're most needed. Then, as the neocortex matures, the modifiable synapses of the basal ganglia provide a vital component of the machinery that supports neocortical learning, both perceptual and motor. Potentiation at the lower end of the circuit supports potentiation at the cortical end.

The hippocampal formation

My guess is that the hippocampal machinery grew out of a mechanism which could correlate longlasting internal conditions such as are registered in the nearby hypothalamus with repeated or ongoing inputs from visual receptors (as processed in the thalamus), or from olfactory receptors. That would mean that the achievement of a satisfactory internal state could come to be associated with the location where it was achieved. The extended input on both sides of the equation would allow plenty of time for synaptic potentiation to develop - which would be the most practical arrangement when external senses were still primitive and only limited data about the external world was being collected. Furthermore a lengthy sampling of the external input would be necessary to ensure that what was registered was a permanent feature of the environment, not just a passing phenomenon.

Learning about the contexts in which desirables such as food or an optimal temperature were usually found would enable the animal to slow down when it reached an environment which provided the cue. The emerging hippocampus can thus be envisaged as complementing the function of the early basal ganglia. Working with widely distributed cues it promoted situations where more proximate cues could be registered.

Communication between hippocampus, basal ganglia and thalamus would bring new potential. The primitive hippocampus expanded into a means of keeping track of the immediate surroundings, and orienting the self in relation to them, using basic visual and olfactory information. The basal ganglia contributed information about cues inviting approach or prompting avoidance, and made it possible to mark places where noxious input had recently threatened, or where all available food had just been consumed. All this, I hypothesise, would be done in co-operation with the thalamus, to

which reports of turns and reorientations would also be forwarded.   The result would be an elementary map of the current surroundings.

The evolution of an effective permanent cognitive map, providing a long-term record of the sites that regularly supplied a fair amount of nourishment or an optimal thermal condition, would require a longer-term memory, and a means of measuring longish intervals of time.   The navigating animal needs to know how long it has taken to get from A to B, and how much effort, and it's helpful, when encountering a landmark for the second time, to have some idea of how long ago the first encounter was.   The hippocampus has the means of measuring such intervals.   But the long-term record of all this information would have to be stored elsewhere, leaving the hippocampal machinery available for mapping new contexts in a way that enabled the more permanent map to be extended in any direction.

So far as I know no brain areas which seem to contribute to a permanent cognitive map have yet been identified in a non-mammal, but the obvious place to look is in the telencephalon, close to the area taken to be the equivalent of the hippocampus.   In the simpler-brained extant vertebrates olfactory cortex takes up another big chunk of the telencephalon.   We can safely assume that some of the remaining area is concerned with weighing up current needs and balancing them against other factors, calculations of the sort that in mammals take place in orbitofrontal cortex.   But some portion of it, I believe, will prove to be taken up by a cognitive map, with equivalents of parahippocampal and retrosplenial neocortex, operating in close association with the thalamus.

From such beginnings we can imagine the hippocampal formation expanding to undertake other functions in an evolving brain.   Building a map essentially involves weaving together information about geographical context with information about some of the things occupying the context, effectively creating a narrative, and thus creating links which make recall possible.   With increasing capacity the narratives came to cover more obviously temporal patterns as well as spatial ones.   As visual systems grew more complex the hippocampus would help in dealing with the more elaborate stimulus patterns, ones which had to be acquired over a series of fixations, or viewed from several view-points for full appreciation.

The hippocampus thus functions as a hub through which information extracted in different cortical areas can be linked.   The links it provides can be reactivated, so that input to one cortical area prompts reference to related information recorded in another area.   This makes the hippocampus essential to conscious recall, or explicit memory.

The amygdala

The definitive fact about the amygdala, I think, is that it's activated by the essential chemical or visual features that define a conspecific, and despatches messages to hypothalamus and hindbrain which evoke hormonal and/or auto-nomic responses.   Some of the communications to the hypothalamus back up signals which go direct from the olfactory and vomeronasal systems.   It may be significant that a small proportion of amygdal neurons are born in the hypothalamus, and migrate to their final position.

A reasonable guess is that, as the number of species expanded and an increasing amount of information was needed to distinguish them, the amygdala evolved to deal with the complexities, duplicating the function previously performed wholly by the hypothalamus, but using more complex information for the purpose.   In many species genetically determined visual and auditory stimulus patterns would come to contribute to the identification of conspecifics, making it easier to identify potential breeding partners at a distance.   These signals would be reported to the amygdala, and their import forwarded to the hypothalamus by much the same channels as the chemical ones.

We can suppose that the amygdala then expanded its role as an intermediary between sensory systems and hypothalamus by evolving sensitivities to other sorts of stimulus patterns for which hormonal responses became useful.   For many it would also be profitable to adjust heartbeat, blood pressure, breathing rate and so forth.   As predators grew more powerful and efficient, genetically determined attentional, hormonal and autonomic responses to threat will have become increasingly

valuable to prey species.   For the predators similar responses to potential prey will have been useful. The amygdal response to cues suggesting food presumably evolved where digestive systems became capable of dealing with more complexly structured food, and could usefully be primed in advance of its arrival.   The amygdala and a closely connected structure also became involved in regulating appetite.   Meanwhile more complicated interactions among conspecifics involved the development of amygdal responses to mates, offspring and rivals.

It's likely that in the first place the stimuli that prompted the amygdal danger response in prey species were odours.   As an alerting signal an odour can be very effective, but it's less helpful at providing a rapid indication of just where the danger is that should be distanced.   The evolution of modifiable synapses in the amygdala would therefore provide a great asset, since it would become possible to learn about stimulus patterns in other senses that were regularly associated with an escape-prompting odour.

The autonomic and hypothalamic responses which, when the results are elevated to consciousness, represent fear have been particularly associated with the amygdala (although at least one other brain area is proving to be significantly involved too).   But the amygdala clearly contributes to learning about several other subjects.   And when mammalian social lifestyles evolved it became worthwhile for faces or voices to become expressive and for the amygdala, already sensitive to conspecific faces, to evolve responses to some of the expressions.   It must be largely due to the amygdala that mammals can learn from the facial and bodily expressions of mother or other conspecifics, in what I've called learning by emotional infection.

The cerebellum

On the evidence of comparative neurology an identifiable cerebellum evolved later than amygdala, hippocampus or basal ganglia.   The part which receives input from the vestibular system and contributes to managing the relationship with gravity is thought to be the oldest bit, so that might have been the cerebellum's first function.   An alternative hypothesis is that it grew out of an arrangement for co-ordinating the defensive responses prompted by local tactile inputs.

Modifiable synapses that make it possible to withdraw from a light contact before a heavier and perhaps harmful one follows are found in modern invertebrates with quite modest nervous systems, so something similar was pretty certainly present in the chordate line from an early stage.   As animals became larger and more mobile the limited reflexive withdrawals effected through direct contacts between sensory neurons and motor neurons can no longer have been adequate for avoiding harmful collisions, so a central device must have become worthwhile.   The mechanism could then have been expanded to integrate these withdrawals with locomotion that distanced the whole animal from the threat.   The advent of a lateral line system would probably give additional value to the machinery, providing the means of retreating from potential tactile inputs before they could happen.

The hagfishes, those distant cousins of all other vertebrates, are the only ones without a detectable cerebellum, and their eyes lack exterior muscles for rotating them, as well as the lenses which would make rotation worthwhile.   The other surviving jawless fish, the lampreys, possess both a detectable cerebellum and rotatable eyes.   This suggests that the expansion of the earliest cerebellar machinery into a definable structure might have coincided with a need to co-ordinate eye movements with body movements.   When bilateral fins appeared the arrangements could be extended further to co-ordinate their deployment with the locomotory ripples along the length of the body.   Directing locomotion will no longer have been merely a business of imposing modifications on the locomotory pattern generator at the right point in the cycle, but will have needed additional proprioceptive feedback, and appropriately timed use of the fins.

A question that suggests itself is whether the existence of a modest cerebellum might actually have facilitated the evolution of lateral fins, and subsequent new body parts.   Was it the learning ability of the cerebellar machinery that made it practicable to add new extensions to the body, the use of which had to be co-ordinated, like escape actions, with the workings of the basic locomotory pattern generator?   Many infant reptiles and amphibians emerge from the egg with clumsy-looking

thrashes and wriggles, which are quickly but not immediately resolved into smoother action. Do those early twitches indicate experimentation as to how the various muscular potentials of the parts can be organised into efficient, co-ordinated movement of the whole? In short, could it be deduced that body extensions were possible because there was a cerebellum which could quickly learn how to manage them, and that the lack of such a facility explains why the ancestors of the hagfishes didn't give rise to a more diverse range of species?

At any rate it may be suspected that the cerebellum was a remarkably fruitful invention. Hagfish, the only species without one, actually have a somewhat larger brain than that of the other extant finless fish, the lampreys, and it has a distinctive, rather squashed-up look. This suggests that in this respect they may have followed a somewhat different evolutionary route from all other surviving vertebrates, one which, though successful in itself, offered much less scope for further developments. The cerebellum certainly proved very versatile, as demonstrated by the fact that it's responsible for the electro-sense of some fish species.

In us and in the great apes - species which have elaborate and adaptable muscle systems and must educate the motor cortex on how to use them effectively – the cerebellum is exceptionally large. It's vital for achieving complex movements smoothly and efficiently, by means of short and therefore fast connections to motor neurons. It's also important in the business of maintaining an upright stance, making use of vestibular information. In addition the cerebellum plays a major role in motor memory, which, as I've stressed, has to be very precise. It's particularly important in the delicate business of uttering speech, and in controlling fine finger movements.

In humans its connections with the neocortex, and especially frontal cortex, are more extensive than would seem to be required for motor control alone, and damage to the cerebellum can produce cognitive problems. Some of these are no doubt attributable to a reduced fluency in language - even internal speech seems to be affected. Perhaps the ability to imagine actions may also be undermined, and with it some of the ability to deal with percepts and ideas that are closely related to action. It also seems possible that where the cerebellum's part in eye movements is compromised visual perception may be affected. Perhaps the cerebellum has a role in other forms of active perceptual exploration too, such as tactile investigation and sniffing. And conceivably it has a role in facial expressions, once they become voluntary. Perhaps it's relevant to remember that cognition has grown out of the means of directing movement, so that the two things, which subjectively seem quite different, are in fact closely interwoven.

Alerting systems

Between them the systems provided a foundation on which it was worth building increased sensory powers - a neocortex in the case of mammals, expanded midbrain structures in reptiles, birds and many fishes. Another major part of the underpinning must have been the evolution of norepinephrine and acetylcholine pathways leading upward from the lower part of the brain. Acetylcholine, the transmitter used by chordates for communication between neuron and muscle, must have been employed from the beginning in the contractions which produced a withdrawal from a potentially noxious input. The same transmitter presumably came to carry a message up to the proto-brain reporting such assaults and preparing the recipient neurons for any further suggestions of danger, and the possible need of larger responses. Norepinephrine perhaps began as a transmitter that influenced the operation of the locomotory pattern generators when such alarm messages were received.

The earliest upward connections were no doubt the ones that go to the hypothalamus and various other nuclei, from which hormonal responses are triggered and the pattern generators of the internal organs controlled. Expansion of these routes, targeted at the developing sensory-processing facilities in midbrain or forebrain, served to ensure that the new machinery was employed where it was most needed.

Visual processing before the neocortex

An implication of all these arguments is that well before the neocortex appeared a fair amount of information was being distilled out of sensory input by the tectum and thalamus. In non-mammalian vertebrates with well-developed visual systems the optic tectum is responsible for a good deal of the data processing, presumably doing much of the job that in us depends on the visual cortex. Even in some other primates many forms of action seem to be more handicapped by damage to the equivalent of the optic tectum, the superior colliculus, than by lesions in visual cortex – though this might be because the superior colliculus is important to guiding attention.

As yet the number of visual operations shown to be performed in primate superior colliculus is limited. The main sensitivity so far demonstrated is to movement, and probably - thanks to input from the neighbouring parabigeminal nucleus - to singularities. But in mice the superior colliculus contributes more to discriminating among different speeds of movement than does primary visual cortex. Mice also have orientation-sensitive neurons in this structure. Something along such lines may yet be uncovered in the primate. And then there is that tantalising idea that the superior colliculus may have the means of registering the archetypal conspecific face.

Similarly, studies of the lateral geniculate nucleus of the thalamus have suggested that in primates it doesn't extract a great deal of information from the retinal input. Some koniocellular neurons record the general distribution of blue light. The magnocellular layers concentrate on moving stimuli. And both magnocellular and parvocellular layers reveal contrasts, but apparently over receptive fields which reveal little about shape. But it's recently turned out that there is a small population of geniculate cells in the marmoset which respond both to orientation (especially vertical orientation) and to movement. Unexpectedly, they are among the tiny cells of the koniocellular layer. They communicate, in turn, to a higher layer of visual cortex than that targeted by the long-known pathways. It seems likely that there is still much to learn about the operations of both lateral geniculate and superior colliculus in primates.

However, it seems possible to sketch out a plausible scenario about how the vertebrate visual system might have begun. The very first photoreceptors employed in vision, simply registering the presence of light, must have served merely to guide an animal towards the light or away from it. They can be supposed to have reported to what would become the thalamus, close to the site of the internal clock which was regulated by the same data.

One possible speculation about the next step is that, perhaps after a gene duplication and a minor modification to one of the duplicates, another sort of photoreceptor appeared, with a maximum sensitivity to a different wavelength. A photoreceptor sensitive to the wavelength reflected by local rocks and stones might have found a function in helping its owner to avoid collisions with hard surfaces, thereby preventing quite a lot of damage. The response needed was a rapid twist away from the danger, so the new receptor would be selectionworthy if its information went to the midbrain site where such actions were organised when they were prompted by tactile input. This site, in what would become the tectum, would expand to receive an increasing amount of visual information, and later auditory information too, as well as the original somatosensory sort.

Further types of receptor, selective for other wavelengths, might find a use in providing a visual cue to the presence of conspecifics, if the species sported bright colours. Each type of photoreceptor may have guided a different sort of behaviour, with a short pathway from receptors to motor neurons. Indeed, the visual guidance of many behaviours may perhaps still be organised in a basically similar fashion in some modern fish and invertebrates, for some species seem to have a large enough range of colour-selective receptors to serve several purposes, without any need for further processing of the colour information.

An alternative hypothesis is that the earliest development in the retina was something akin to an OFF-centre ganglion, capable of combining the data provided by several photoreceptors and detecting an edge between dark and light. That too might provide a cue to the presence of something hard, to be avoided. An interesting wrinkle in the visual system is that OFF neurons operate more effectively than ON ones, so that dark stimuli can be seen with somewhat greater spatial resolution

than light ones.   The OFF neurons also relay their information more rapidly.   If, in early days, dark stimuli represented nearby dangers to be avoided as quickly as possible and light merely functioned to guide the slower business of locomotion, then efficiency in registering the former would have been more important.   ON and OFF pathways do indeed serve different ends in zebrafish larvae, which are hardwired to swim towards light. The OFF pathway runs to the tectum, where it prompts turns away from dark areas.   The ON pathway contacts serotonin neurons, causing an acceleration towards the goal.

One thing that seems certain about the first retinal ganglion cells is that they will have responded only to local contrasts, for there will have been no means of focussing a distant image on the retina - obviously there was no mileage in evolving such a mechanism before contrasts could be detected.   It's likely, moreover, that the new device was sensitive only to moving contrasts, since the visual stimuli an animal really needs to know about are the ones that are moving in relation to the retina, whether the movement is attributable to the object or produced by the animal's own motion. An ability to detect moving contrasts would have vastly improved the collision avoidance system.   It might have been one of the advances that made it practicable for somewhat larger animals to evolve.

As the variety of wavelength selective receptors and contrast-detecting neurons increased a potential will have opened up for guiding other forms of behaviour by vision, such as the search for food.   Then yet further additions to photoreceptors or contrast-detectors would be useful.   By this time, of course, any development that helped to focus the incoming light rays, a lens or a cornea, would also have brought benefits.

A little data from contrast-detecting ganglion cells, and possibly a little about colour, had perhaps been going to the thalamus as well as the tectum.   There it would provide information about visual textures that could be used by the primitive hippocampus, which might be correlated with information about internal states from the hypothalamus.   Only when a focussable lens evolved would it be possible to collect data about distant contrasts, and to detect distant landmarks, which could be used for guiding locomotion.   At this point it would become worthwhile to report rather more visual data to the thalamus, and eventually, as vertebrate brains grew more complex, to the telencephalon.

In other words I think that there are essentially two visual systems.   One evolved to manage local reorientations and actions on nearby objects, the other to direct locomotion to more distant targets.   In many species the optic tectum is still the important structure for organising actions on nearby visual stimuli.   But I think it's a thalamic pathway that guides travel.   The hypothesis fits neatly with the fact that there are two centres for releasing locomotion, and the idea that one deals in locomotion to distant areas, the other in approaching nearby stimuli.

Many lifestyles might be managed quite satisfactorily with a limited degree of co-operation between two such visual systems and two locomotory centres.   A much tighter knitting together of the thalamic and midbrain functions may be one of the things achieved by a neocortex.