Cooperation of the basal ganglia, cerebellum, sensory cerebrum and hippocampus: possible implications for cognition, consciousness, intelligence and creativity

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Abstract

It is suggested that the anatomical structures which mediate consciousness evolved as decisive embellishments to a (non-conscious) design strategy present even in the simplest unicellular organisms. Consciousness is thus not the pinnacle of a hierarchy whose base is the primitive reflex, because reflexes require a nervous system, which the single-celled creature does not possess. By postulating that consciousness is intimately connected to self-paced probing of the environment, also prominent in prokaryotic behavior, one can make mammalian neuroanatomy amenable to dramatically straightforward rationalization. Muscular contraction is the nervous system's only externally directed product, and the signaling routes which pass through the various brain components must ultimately converge on the motor areas. The function of several components is still debatable, so it might seem premature to analyze the global operation of the circuit these routes constitute. But such analysis produces a remarkably simple picture, and it sheds new light on the roles of the individual components. The underlying principle is conditionally permitted movement, some components being able to veto muscular contraction by denying the motor areas sufficient activation. This is true of the basal ganglia (BG) and the cerebellum (Cb), which act in tandem with the sensory cerebrum, and which can prevent the latter's signals to the motor areas from exceeding the threshold for overt movement. It is also true of the anterior cingulate, which appears to play a major role in directing attention. In mammals, the result can be mere thought, provided that a second lower threshold is exceeded. The veto functions of the BG and the Cb stem from inhibition, but the countermanding disinhibition develops at markedly different rates in those two key components. It develops rapidly in the BG, control being exercised by the amygdala, which itself is governed by various other brain regions. It develops over time in the Cb, thereby permitting previously executed movements that have proved advantageous. If cognition is linked to overt or covert movement, intelligence becomes the ability to consolidate individual motor elements into more complex patterns, and creativity is the outcome of a race-to-threshold process which centers on the motor areas. Amongst the ramifications of these ideas are aspects of cortical oscillations, phantom limb sensations, amyotrophic lateral sclerosis (ALS) the difficulty of self-tickling and mirror neurons. © 2001 Elsevier Science Ltd. All rights reserved.

Contents

1. Introduction

It is often said that elephants never forget, though one might ask what an elephant actually has to remember. The biological answer is straightforward, an elephant has to remember no less and no more than any other creature which ever lived. For the fact is that all creatures, great and small, have only ever had to remember one thing, how to move under the prevailing circumstances in their environments and within their own bodies. Movement is the sole means by which any creature can actively secure the wherewithal for its survival, and Sherrington (1924) perceived this when he wrote: *To move is all mankind can do, and for such the sole executant is muscle, whether in whispering a syllable or in felling a forest.*

Given this primacy of movement, it is surprising that more attention has not been paid to the words of another prominent physiologist. As Sperry (1952) noted:

> *An analysis of our current thinking will show that it tends to suffer generally from a failure to view mental activities in their proper relation, or even in any relation, to motor behavior. The remedy lies in further insight into the relationship between the sensori-associative functions of the brain on the one hand and its motor activity on the other. In order to achieve this insight, our present one-sided preoccupation with the sensory avenues to the study of mental processes will need to be supplemented by increased attention to the motor patterns, and especially to what can be inferred from these regarding the nature of the associative and sensory functions. In a machine, the output is usually more revealing of the internal organization than is the input.*

The line taken in the present communication will be even more radical than the one recommended by Sperry. It will be argued that our main focus should indeed be on the animal's output, and that a proper understanding of the neurobiology can best be gained from what almost amounts to a preoccupation with the motor avenues.

In the deepest sense, this paper will be asking what possession of a brain actually does for an animal. And although an exhaustive discussion of evolution lies beyond the ambitions of the text, we will be touching upon various evolutionary mileposts, and noting that the underlying behavioral strategy of Earth's creatures does not appear to have changed in the four billion or so years since they sprang from their last common ancestor (Collins and Jegalian, 1999).

This new insight, if that is what it proves to be, will have been gained primarily from a desire to compile an unusually comprehensive circuit diagram of the brain, and of the related components of the nervous system. This is only now becoming feasible, and it has been made possible by the skills of those who trace the connections between the brain's various regions. These details, and their sources, are described and cited in the paper's third section. We will find that a focussing on the motor output is indeed supported by the underlying anatomy, because the various signaling routes appear to converge on the frontal lobe's movement-mediating areas, that is to say the primary motor cortex (M1), the premotor and supplementary motor cortices, and the prefrontal cortex (PFC).

These anatomical details having been introduced, it will be suggested that the three main movement-provoking (as opposed to movement-*mediating*) streams in higher animals actually function cooperatively, and that the overall situation probably admits of various scenarios. When the cooperative mechanism is working at full strength, it will be argued, the result is overt movement. But it will be suggested that there is also a lower-threshold mode of brain activity which corresponds to a covert form of movement, intimately connected with thought. This line is in harmony with what Ritchie (1936) was advocating when he noted: *I find it hard to see why thinking with nothing should be more truly thinking than thinking with your muscles. Because think-ing is mental it does not follow that it is not bodily too.*

The paper will suggest that considerable advantage could accrue from embracing its alternative views. These offer a rather straightforward way of defining cognition, for example, and they lead to a new view of consciousness, which is seen as enabling an animal to acquire novel context-specific reflexes. In passing, this idea will lead to a reappraisal of the role of the hippocampus, and of the dreaming state. Moreover, this new theory provides an account of intelligence which is attractively transparent. Finally, and in addi-tion to shedding new light on a number of ancillary issues, it suggests a physiological origin for a particu-larly ill-defined attribute, namely creativity.

2. Unconscious cognition in lower species

2.1. Stimulus and response in primitive organisms

Unicellular organisms do not possess nervous sys-tems, of course, but it might be supposed that they have rudimentary counterparts of reflexes; it would be logical to assume that gradients of environmental substances would elicit appropriate motor responses. In his classic investigation of bacterial swimming, Berg (1993) showed that this is not the case. A bacterium like *Escherichia coli* is unable to gauge such spatial varia-tion, at any instant, so it procures information by probing its surroundings, through the propulsion pro-vided by its flagellum. In effect, this creature integrates incoming chemical signals during a few-second period of its travels, and adjusts its direction of advance accordingly. The integration is achieved through tem-porary chemical modifications to molecules located in the bounding membrane, which transfer nutrients to the cytoplasm, and also through changes to certain other molecules in the interior of the cell. Such integra-tion is essentially a short-term memory mechanism (Eisenbach, 1996). The stimulus in this microscopic expedition is thus the motor movement, while the re-sponse is that of the impinging substances. This is just the opposite of a reflex.

This mode of behavior is so fundamental that it is worth considering the details, as they are seen in *E coli*. The situation is illustrated schematically in Fig. 1. The cell's membranes are equipped with receptor molecules (not to be confused with the receptor *cells* discussed later) each of which has an extra-cellular domain that binds amino-acid ligands directly (or sugar ligands indi-rectly) when they are bound to a specific small protein
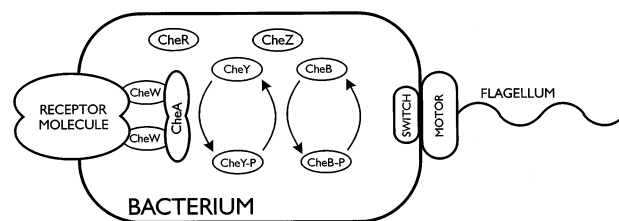
Fig. 1. The behavior-determining components in the *E. coli* bacterium are indicated in this highly schematic diagram, in which no effort has been made to faithfully reflect the relative sizes. The direction of rotation of the creature's flagellum is determined by the concentra-tions of the various molecular species, these concentrations mediating a primitive form of memory. The bacterium gains information about its surroundings through its own movements.

(a ligand being a small molecule, or part of a small molecule, which interacts with a larger molecule, such as a protein molecule). The inner region of the membrane-spanning receptor molecule favors interaction with the coupling protein designated CheW, as well as with a kinase designated CheA. The latter transfers phosphate from the energy transporting molecule ATP to two other proteins, known as CheY and CheB. CheY is the effector of the bacterium's flagellar motor (Magasanik, 1995; Macnab, 1995, 1996; Stock and Surette, 1996).

The binding of an attractant ligand to the receptor molecule's external domain decreases the activity of the kinase, and this in turn leads to a decrease in the amounts of CheY-P and CheB-P that are being made. CheY-P's signaling action proceeds by its diffusing through the cytoplasm and by its binding to a component of the flagellum known as the switch (designated FliM). This binding increases the probability that the motor will spin in the clockwise direction. Because forward motion is produced by an *anti*-clockwise rotation of the flagellum, such clockwise rotation causes the cell to tumble and the ultimate result is that the creature then swims in a different direction. When the cell is swimming in the direction of increasing attractant concentration, therefore, more attractant becomes bound to the receptor molecule's external domain, less Chey-P is produced, less of this substance binds to the switch, and the bacterium continues its forward movement. There are a number of different categories of receptor molecule, and they activate the kinase to varying degrees. This differential mode of functioning imbues the system with the ability to integrate the incoming chemical information, the product of that integration determining the concentration of CheY-P in the cell's cytoplasm.

In addition to these primary mechanisms, there is an adaptation process which increases the range of sensitivity. A methytranferase, designated CheR, slowly methylates the inner domain of the receptor protein when the kinase activity has been reduced by the binding of attractant ligands. This tends to restore the activity of the kinase, even when the ligand remains bound. Cells exposed to a sudden change in ligand concentration will thus tend to recover, and continue with their current mode of swimming. CheB is a so-called methyesterase, which detaches methyl groups from certain molecules. It is more active when it is phosphorylated (that is to, say when a phosphate group is attached to it), and it appears to act on receptor molecules only when they are in a kinase-active state. In effect, this enables the receptor molecules to compare the occupancy of their ligand binding site—a measure of the current conditions in their local environment—with the occupancy of their methylation sites—a measure of past conditions— and activate the kinase
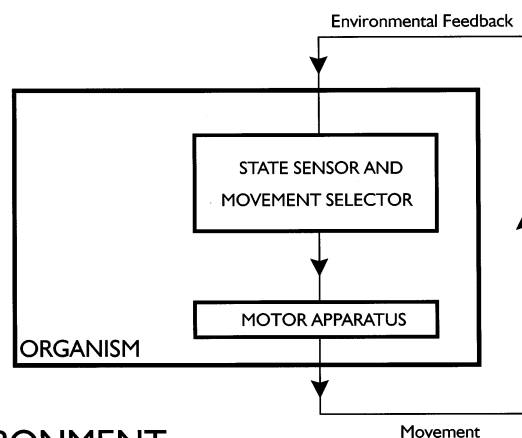
Fig. 2. The behaviour-determining system in the bacterium shown in Fig. 1, and in similar primitive creatures, can be rationalized as shown here. There are no senses, of the type found in more advanced species, and the internal state of the creature is embodied in the concentrations of various molecules. These concentrations dictate the creature's movements.

in proportion to the measured difference. There is also a phosphatase, designated CheZ, which removes phosphate from CheY-P, thereby shortening its lifetime.

The upshot of these various condition-dependent chemical reactions is to imbue the cell with a short-term memory spanning about 4 s, with the concentration measured over the past second being compared with the concentration measured over the previous 3 s, with positive and negative weighting, respectively (Segall et al., 1986).

It might seem out of place to have described these reactions in such detail, in a text purporting to aim at rationalizing brain function, but the main thrust of the present communication is that the basic behavioral strategy (unconsciously) employed by this lowly creature has its counterpart in all more advanced species, including those which possess consciousness. And comparisons with those higher animal forms will be facilitated by the use of the type of diagram shown in Fig. 2, which pares the bacterial system down to its essentials. This creature's motor apparatus is, of course, its flagellum, while the various sets of chemical reactions collectively monitor the state of the system and select the appropriate mode of movement, that is to say anti-clockwise or clockwise rotation of the flagellum. And it is worth reiterating that the relevant stimulus is the bacterium's movement, while the relevant response is that of the environmental feedback. We are ultimately going to see that this reversal of the traditional stimulus-response scenario has relevance even for consciousness itself.

We did not descend from bacteria. They were one product of the evolutionary bifurcation from the universal ancestor, some four billion years ago. The other

branch, that is to say the archaea, was also prokaryotic (i.e. devoid of a nucleus), but it ultimately gave rise to the eukaryotes (which possess a nucleus)-initially the protozoa and later the higher life forms. There is much evidence that electrochemical signaling appeared quite early on the evolutionary scene (Spencer, 1989). Motility in the protozoa resulted from the interaction of fibrillar proteins with calcium ions and ATP, and it has been shown that directional control of flagellar beating in *Euglena gracilis* is dependent on changes in the internal calcium concentration (Febre-Chevalier et al., 1989). In *Paramecium*, a typical member of the somewhat more advanced unicellular organisms known as ciliates, one sees a resting membrane potential that is not dissimilar to that observed in vertebrates; it lies around -50 mV and is potassium-dependent. That there is actual electrochemical signaling in this creature is attested by the fact that ciliary reversal has been demonstrated to be linked to membrane depolarization and change in calcium-ion concentration (Wood, 1970; Hennessey, 1989). Another participant commonly found in the nervous systems of more advanced creatures, namely the so-called second messenger, cyclic-AMP, also plays a major role in the behavior of *Dictyostelium* (Van Houten, 1989). When the amoebae of this species run out of bacteria to feed upon, they consolidate into a multicellular slug by responding to pulses of cyclic-AMP.

An early evolutionary embellishment involved addition of non-chemical receptors, such as the chlorophyll-based variety possessed by *Euglena*. By detecting a factor in the environment (in this case sunlight), these molecules impose an additional bias on the creature's movements. The situation is nevertheless the one illustrated in Fig. 2, and the creatures of that evolutionary period did not possess what we would call senses. But as we have just seen, a trend had been set whereby there was a speeding up of the transfer of information. This involved augmentation of (slow and weakly directed) chemical diffusion with (fast and strongly directed) electrochemical signaling. Ultimately, about 700 million years ago (Anderson, 1989), one sees the emergence of actual nerve cells. Instead of merely being deployed on the organism's bounding surface, the receptor molecules became incorporated in the membranes of the multicellular creature's specialized receptor *cells*.

The first actual nervous systems seem to have appeared with the Cnidaria, that is to say the hydroids, jellyfish, sea-anemones and corals (Anderson, 1989). These creatures possess well-defined neurons, and chemical synapses are much in evidence. But even in the great majority of these, the overall behavioral strategy still appears to be that depicted in Fig. 2. Most jellyfish, for example, are able to avoid noxious substances in their environments, but their reactions are of the slow, bias-modifying type seen in lower species. In two types

of jellyfish, however, one can observe two clearly *different* modes of behavior (Meech, 1989). The species in question are *Aglantha digitale* (Donaldson et al., 1980) and *Amphogona apicicata* (Mills et al., 1985). In *Aglantha*, one sees a dual repertoire of swimming modes, a slow feeding mode being supplemented by rapid escape swimming (Mackie, 1980). Mackie and Meech (1985) demonstrated that these two modes were mediated by two different types of propagating nerve impulse and not, for example, by two different types of muscle fiber. It would be possible for this situation to be captured by Fig. 2, the different swimming modes being dictated merely by what has been termed the movement selector, but it seems more likely that the situation had by this time advanced to the one depicted in Fig. 3; *Aglantha*'s ability to escape from predators appears to be a reflex.

In any event, one certainly sees reflexes in creatures evolutionary senior to the cnidaria, such as the arthropods, mollusks and annelids. Kandel's studies of the aquatic mollusk *Aplysia* (1976), for example, document an impressive repertoire of rapid reactions, and the underlying neural circuitry is actually suggestive of the more complicated situation depicted schematically in Fig. 4. The nervous system of Aplysia can be rationalized by according it a rudimentary form of sensory processor.

Given the relative simplicity of the reflex, it must have evolved relatively rapidly, and at a certain stage it must have acquired its well-known potential for autonomy, a receptor cell's reaction to an unprovoked stimulus leading unaided to a motor response. Refinement and improvement of the probe-by-movement mechanism, unavoidably dependent on detection of environ-
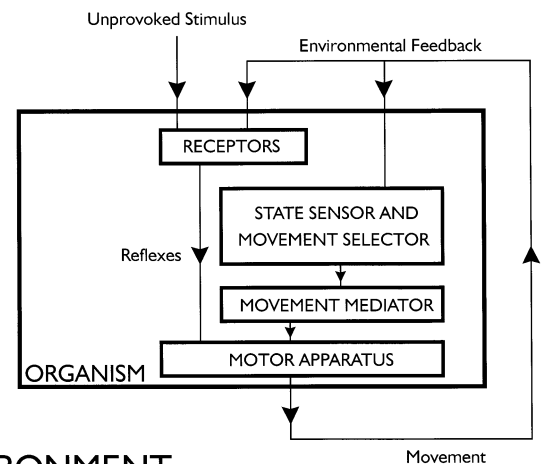
Fig. 3. With the advent of nerve cells, the behavioral repertoire of even relatively primitive creatures became impressively diverse. This diversity stemmed from the emergence of a neuron-based mediator component, different motor programs being achievable through different patterns of connections between its constituent cells. A particularly important innovation was the reflex, which produced a motor response independent of the creature's internal state.
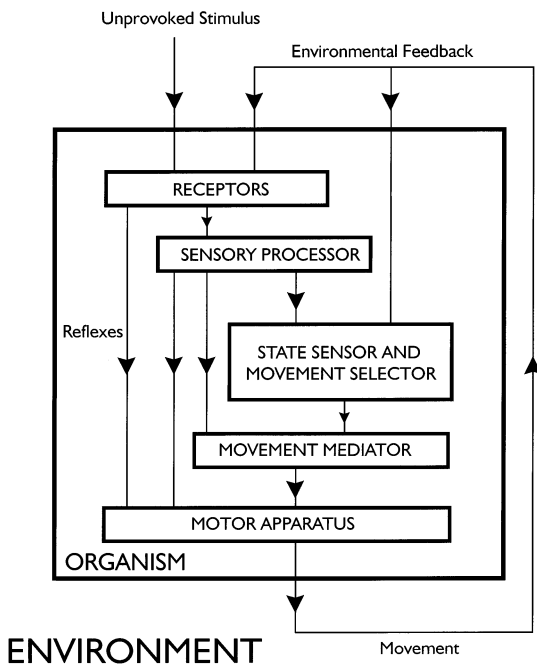
Fig. 4. A further embellishment made possible by the emergence of nerve cells was the sensory processor. It permitted the capture of correlations between different sensory inputs, these being tied to motor output after varying degrees of intermediate processing.

mental feedback, could not have been more rapid because that detection was perforce also predicated on the development of receptor cells. Ultimately, the probe-by-movement mechanism appears to have spawned two sub-mechanisms, one overt, a direct descendent of that seen in unicellular organisms, and the other covert, a probe-by-*proxied*-movement. One of the chief aims of the current communication is to explore that latter faculty, and identify it with consciousness. It will be argued that it serves the system in a sophisticated fashion, by permitting modification of reflexes in a context-dependent manner. Indeed, it will be argued that such modification is the *raison d'etre* of consciousness. But there is much more to be considered before we can essay a discussion of such lofty concepts; we should pause here and consider the possible applicability of certain familiar concepts and terms to the lowly creatures we have been discussing.

2.2. Purpose, information and cognition

Given this tracing of movement-related processes to their evolutionary roots, what is the relevance of words such as *purpose* and *cognition* to the primitive creatures we have been discussing? Because energy is required for metabolism and reproduction, it seems that purpose can be granted to such organisms (Jennings, 1933), albeit in an unconscious form. Purpose logically gives rise to *volition* in the conscious creature, but not otherwise, according to the dictionary definition (Onions,

1962). The word *information* poses no problem because it relates to the organism's purpose and the local attributes of its surroundings; it is clearly related to the concentrations of substances in the environment and within the body. It can also be related to objects (such as predators) detectable at a distance in the environment, but only if there is the facility for remote sensing. An organism has *knowledge* of its environment if it is apprised of such information, though that acquisition might be unconscious. The *meaning* of a situation can be gauged against current information, again without consciousness as a prerequisite; the words *meaning* and *significance* are clearly tied, in this context. This suggests that the word *cognition* itself has no mandatory bond with consciousness, though there is naturally a conscious version (Århem and Liljenström, 1997).

As we have seen, the direction of rotation of a bacterium's flagellum is reversed when the concentration of certain molecules falls below a threshold value (Macnab, 1995), the creature's behavior thereby switching from one mode to another. The criterion for a cognitive event having occurred can be based on such a behavioral change, though for advanced creatures these changes might be either actual or merely potential. We may thus postulate that cognition is linked to an animal's motor output, rather than to its sensory input. This is, of course, in keeping with the main thrust of this communication.

Some organisms perpetually do everything they are capable of, as when *E. coli* is grown on glycerol (though not on glucose). The activity level varies in more advanced creatures, the (unconscious) drive being determined by their needs and the current internal availability of resources (Sinnott, 1950). That impetus translates into overt motor movement when it exceeds a certain threshold. If a creature has a nervous system, such threshold-exceeding events provoke the appropriate action, again with no obligatory involvement of consciousness. In a creature capable of it, consciously-generated drive would become *motivation*, the dictionary definition being 'that which invites the mind to volition' (Onions, 1962).

This discussion of various terms has not been otiose speculation. If it really is the case that cognition can be defined in the bacterium, for example, this would have great value because of that creature's relative simplicity. Its body consists of so few components that there would seem to be the possibility of getting right to the heart of the matter. Above all, because the bacterium possesses no nervous system, we would glimpse the chance of endorsing Sperry's above-cited dictum to a degree which even he might have found surprising.

The balance of this communication will be predicated on that possibility, for it will be suggested that cognition is always more intimately related to an organism's movement than to its sensory input. Indeed, it will be

suggested that the concept of sensing may be in serious need of re-evaluation. And the ultimate prize offered by such a change of paradigm, it will be suggested, could be the resolution of a particularly refractory aspect of the mind-body problem, where is the actual *seat* of the mind? If the analysis presented here is valid, the mind would be exposed as being inextricably related to the body, and the much-vaunted mind-body problem would have been unmasked as a sham. These are strong words, of course, and yet they follow logically from that attribution of cognition to organisms devoid of nervous systems. For in such creatures, cognition involves monitoring of the state of the body *by* the body. If this is true of *all* creatures, even those possessing consciousness, the attractive possibility would arise that even consciousness itself involves nothing other than an analogous monitoring of the body by the body, the additional trick being that the nervous system permits this to be accomplished in a covert manner.

2.3. Some pertinent evolutionary developments

Although, as mentioned earlier, this communication does not aim at an exhaustive chronicling of subsequent developments of the nervous system, it will be useful to touch upon certain features which emerged after the cnidarians. The next major branching produced three phyla, the annelids (ringed or segmented worms), the molluscs (of which the above-mentioned *Aplysia* is an example) and the arthropods (crabs, insects, spiders, centipedes, etc.), the latter phylum being the largest in the animal kingdom, in terms of the number of species it comprises. Fig. 5 is a schematic representation of part of the nervous system of one of these, namely the honeybee. It highlights components associated with olfaction, and emphasizes those that participate in reward learning (Hammer, 1997). Such learning produces conditioning of what is known as the proboscis-extension response (designated PER in Fig. 5), but the figure reminds us that in this case too the so-called response can just as logically be regarded as a stimulus (that is to say, a producer of environmental feedback). The mushroom body, with its associated alpha and beta lobes is now regarded as a protocerebrum (Borst, 1999).

The really significant feature of Fig. 5, in the present context, is the premotor region. This cannot be encompassed in the scheme shown in Fig. 4, because the latter has but a single motor unit (designated the movement mediator) before the actual motor apparatus. Given that the latter consists exclusively of the muscles, that single movement mediator is analogous to what is usually referred to as the motor cortex in higher species. The honeybee's motor apparatus is not shown explicitly in Fig. 5, so the parts labeled 'motor' (including the PER region) are to be regarded as the creature's motor 'cortex'. The premotor region, including the PER-serv-

ing lateral protocerebral lobe (LPL in Fig. 5), codes for motor *sequences* rather than for individual muscular movements.

As is well known, the honeybee can reliably measure the distance to a source of nutrient, and pass on this information to its hive-mates, by means of its waggle dance. Von Frisch (1993) believed that the distance was measured in terms of the absolute energy consumption, but Srinivasan et al. (2000) have demonstrated that the bee actually gauges the amount of visual variation experienced during the successful forage, and uses this as the indicator of distance traveled. So here too we find movement acting as the stimulus, while the environmental feedback is the pertinent response. And it is difficult to imagine the honeybee being capable of its waggle dance if it could not draw upon the motor-sequencing capability provided by the premotor region.
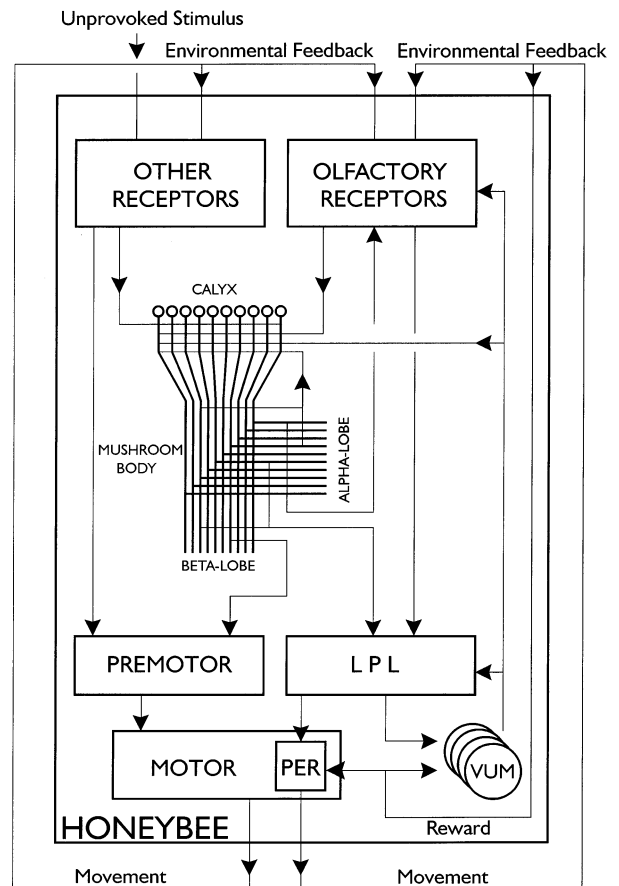
Fig. 5. The motor apparatus is merely implicit in this highly schematic illustration of part of the honeybee's nervous system; the unit marked 'motor' is equivalent to 'movement mediator' shown in Fig. 4. It may be regarded as a forerunner of the motor cortex found in more advanced species. Particularly noteworthy features are the premotor unit, which permits selection of *sequences* of muscular movements, and the behaviour-modifying reward system. The abbreviations are: LPL, lateral protocerebral lobe; PER, proboscis extension response; and VUM, ventral unpaired medial neurons.
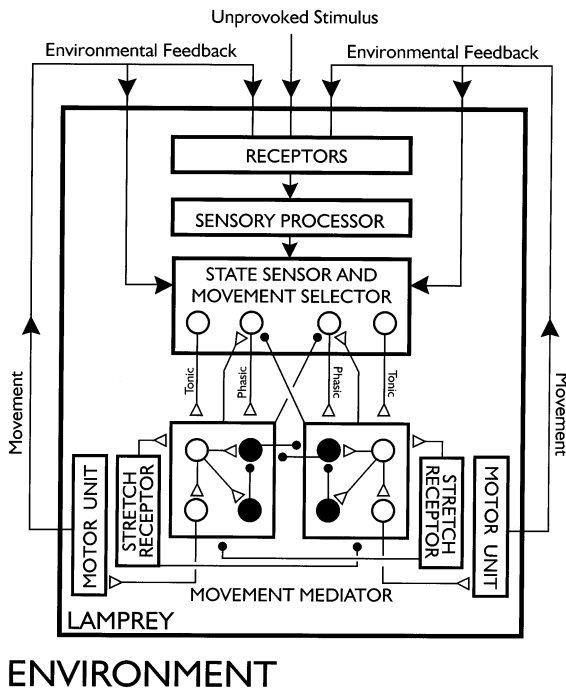
Fig. 6. The rhythmic waggle of primitive vertebrates, such as the lamprey, is provided by the crossed inhibition between the counter-disposed groups of neurons illustrated schematically within the box-pair marked 'movement mediator', there being about a hundred such pairs distributed along the length of the body. Excitatory neurons and their synapses are indicated by the open circles and triangles, while their inhibitory counterparts are shown as large and small black circles. The synapses shown as contacting the boxes, rather than individual neurons, exert more widespread influence. The primitive stretch receptors may have been the forerunners of the muscle spindles now found in more advanced species.

The subphylum Vertebrata (of the phylum chordata), which emerged about 450 million years ago, divided into the agnathans and the gnathostomes (Northcutt, 1981). The former are now represented by very few species, such as the lampreys and the somewhat older hagfishes (Northcutt, 1984). Although anatomical investigations of these species is still at an early stage, there is solid evidence of a (divided) cerebrum and thalamus. The lamprey can be regarded as a prototypical vertebrate and it offers the experimental advantage of having a nervous system which comprises orders of magnitude fewer neurons of each type than higher vertebrates (Grillner et al., 1989, 1995). Fig. 6 includes a highly schematic illustration of a small portion of the lamprey's central pattern generator (CPG), there being about a hundred paired units distributed uniformly along the length of the body. The regular waggling locomotion is made possible by the crossed arrangement of the connections between the excitatory neurons (the large white circles and white triangles representing the soma and the associated synapses, respectively) and inhibitory neurons (large black circles and small black circles).

According to the nomenclature we have been using thus far, the hundred or so pairs of units collectively constitute the movement mediator, the cells which feed excitation to the motor units (that is to say, the muscles) being the motoneurons. The activity level of the cells in the CPG units is controlled by the reticulospinal neurons, which project from the lower brainstem to the spinal cord. It is interesting to note that the regular left-right-left-right alternation seen in normal locomotion can be interrupted by a tonic burst from an appropriate sub-set of these neurons. The creature thereby (unconsciously) alters its direction of swimming. It is fascinating to note that this is simply a more sophisticated counterpart of what was described above in connection with the bacterium.

In the normal locomotory mode, there is a phase delay of about 1% of the cycle duration between adjacent pairs of units. This regularity is also served by the crossed excitatory and inhibitory influences stemming from the stretch receptors, these influences being strictly local. In higher vertebrates, one finds muscles in which the stretch receptors are an integral part of the muscles themselves, the receptors being incorporated in the so-called spindles (Matthews, 1972, 1982), and in the mammals there are routes via which signals from these spindles are dispatched to various regions of the brain. One could say that in mammals, therefore, the influence of the stretch receptors is no longer merely local. As will be noted later, when we consider mammals in more detail, the wider broadcasting of the messages from the spindles may serve the much more varied repertoire of movements which these creatures have at their command.

The ultimate evolutionary product was the brain itself, though there is not universal agreement as to why this structure actually developed. One obvious view is that it served to gather the sensory organs and their interneurons into a single unit, an alternative idea being that its precursor emerged at a primitive stage, as a device for coordinating the two sides of the body. This latter view is not inconsistent with what was discussed above in connection with the lamprey, because although the two halves of each paired unit act upon each other in an autonomous manner, they nevertheless require the appropriate guidance from the upper reaches of the nervous system. In other words, and as Koopowitz (1989) has stressed, the peripheral reflexes can act independently of the brain, but they can also be coordinated and sequenced by it. The main point to be grasped here is that the brain's primary purpose lies in the need for inhibiting peripheral reflexes, when particularly sophisticated sequences of muscular movements have to be executed.

This is indeed suggestive of reflex scenarios far more nuanced than those we considered in connection with the lamprey, and it asks what would be involved in the

gaining of a new reflex during an animal's lifetime. If the animal is *Aplysia*, this need involve no more than simple habituation or pairing of stimuli, as that work of Kandel (1976) showed. But we have just been emphasizing the importance of *sequences* of muscular movements, so we must ask what might be involved in the appropriation of new *context-specific reflexes*, that is to say reflexes which are galvanized into action only when triggered by the correct sequence of elements in the environmental feedback. One of the major themes in the present communication is that such acquisition makes surprisingly large demands on a nervous system, and that it is possibly seen only in the mammals (though perhaps also in the birds). In fact, we will argue that it actually requires consciousness, which thus becomes the *raison d'etre* of the phenomenon. Before this hypothesis can be evaluated, however, it will be necessary to consider the details of the issue to which we must now turn, mammalian neuroanatomy.

3. Anatomical connections to the motor areas

Fig. 7 is the central illustration of the present communication and it is reproduced in color, in an effort to facilitate contemplation of its wealth of detail. The figure reflects mammalian anatomical position only approximately, though nothing has been so grossly displaced as to cause confusion. The green lines indicate excitatory routes, though naturally not individual axons, while the red routes are inhibitory. The solid black lines to the upper right of the figure indicate routes of a more general type, associated with the autonomous nervous system. The black dotted lines have been reserved for processes which involve the environment, examples of these being the fast feedback associated with reafference (seen at the lower left), the input which is not provoked by the organism's own movement (at the lower center), and finally the slow feedback which primarily makes its impact via the vascular system rather than through the sensory receptors (along the left-hand edge). The immediacy of reflexes is suggested by the thick green lines at the lower edge of the figure. Eye responses are triggered by the superior colliculus, rapid variants being represented by their own thick green line. But as for all movements, gaze shifts can follow also after various degrees of deliberation (Carpenter, 1994). They and their counterparts elsewhere in the system are the complicated reflexes which are our main concerns here. As mentioned in the previous section, we need to ask what serves their acquisition, and the point can be made immediately that this is inextricably tied to the probe-by-movement mechanism whereby the environment is explored.

Tracing the signaling routes serving that mechanism is more difficult, though its central link is clear enough,

the fast feedback from the environment. An example of slower feedback is that which alters blood sugar concentration through the muscular movements involved in finding and consuming food. The subtlety lies in following the paths that ultimately lead to the muscles which provoke feedback. Now it turns out that *this goal is simplified by a remarkable parallel with the situation discussed above for primitive organisms, because for both they and the mammal the overall mechanism mediates choice between permitting the current movement, switching to another, or stopping altogether*. This is the simplifying theme which the present communication seeks to present. And if it can be accepted that cognition is unavoidably linked to movement, in either an overt or a covert form, there is the prospect that the story can include a description of mental processes as well. But before that can be contemplated, it will be necessary to consider the underlying anatomy. Let us now get down to a detailed account of the components shown in Fig. 7.

3.1. Connections from the basal ganglia (BG), anterior cingulate and related regions

The connections between the various units in the BG (and the cerebellum (Cb)) are critical, as are the manners in which these are connected to the appropriate thalamic nuclei. The latter's projections to the motor areas are clearly of equal importance. The influence of a given movement on possible subsequent movement is no longer exerted exclusively through the relatively simple components depicted in Figs. 2 and 3. And we see that even Fig. 4 is inadequate because it does not include the counter-running connections through which the motor areas feed signals back to the sensory areas. We also note that the state sensors shown in those three earlier figures have developed into a rather complex system; there is the relatively slow signaling via the vascular system, which interfaces with much faster neuronal components via the hypothalamus. The hypothalamus does not dictate muscular movement directly because there must be a counterpart of the bacterium's molecular-level decision processes. Instead, it sends signals to the amygdala, which acts upon the BG. The latter play a clutch-like permissive role, disinhibition being a common feature of the circuitry (Goldman-Rakic and Selemon, 1990). There is a sad similarity between one symptom of Parkinson's disease and the jerky clutch control of the novice motorist.

The clutch analogy is incomplete, however, because the BG are subject to other influences; other brain components contribute to the adjudication function. This introduces something not present in the bacterium, attention. The direction of a bacterium's flagellar motion is determined solely by the molecules influencing the rotor, whereas the system illustrated in Fig. 7 can
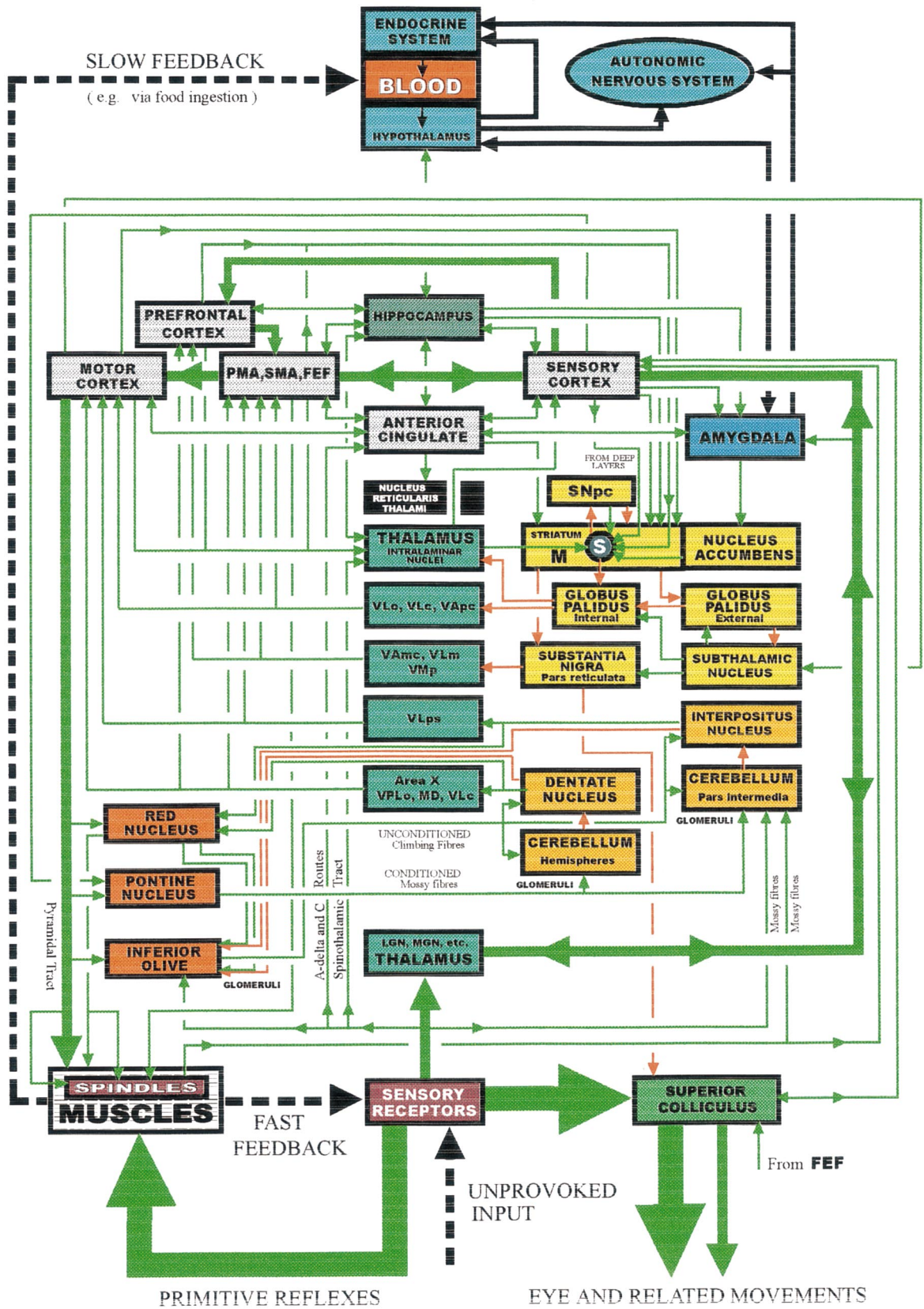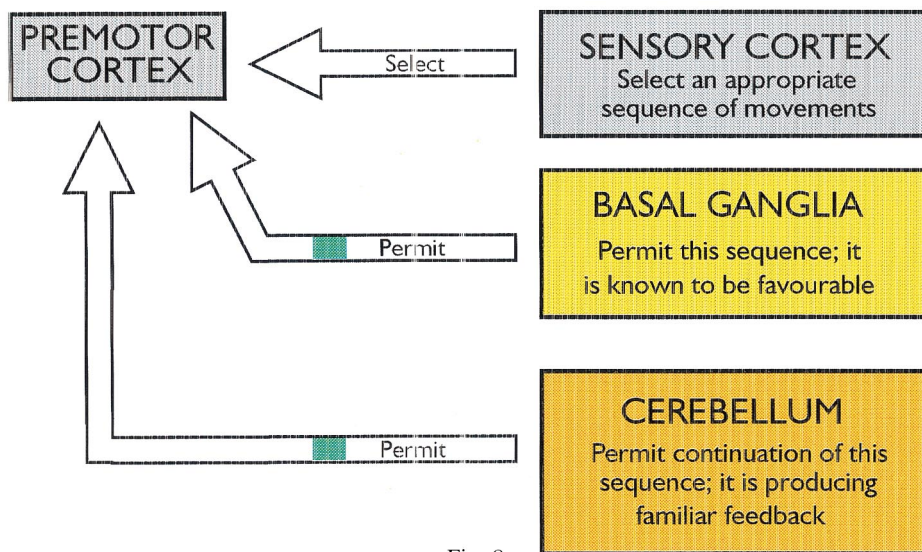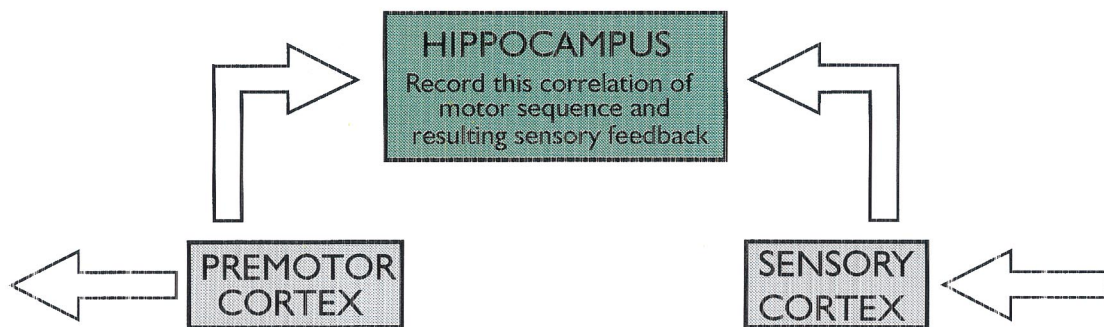
Fig. 7.

Fig. 8

Fig. 9

Fig. 8. The roles of three of the components shown in Fig. 7 are indicated here, the color code being the same as in that other diagram. If the ideas put forward in the present communication are correct, the influences on the premotor area are selection of a suitable sequence, by the SC; permission to execute the sequence, by the BG; and permission to continue the sequence, by the Cb. The influences on the SMA and the PFC would be expected to be rather similar.

Fig. 9. The role of the hippocampus is indicated here, the color code again being the one used in Fig. 7. If the ideas advocated here are correct, the hippocampus records correlations between motor sequences and the resulting sensory feedback, and stores them temporarily. It subsequently mediates establishment of a more permanent record in the cortex itself, this becoming the basis of declarative memory.

shift its focus, and thereby influence its own decisions. That is not to say that the shift of attention is always consciously willed; we have to allow the possibility that this happens automatically, in a manner sometimes referred to by the term *bootstrapping*.

This issue is as recondite as it is important, so we

should pause here and consider how it is investigated experimentally. A well-tried approach involves what is known as a Stroop interference test (Stroop, 1935; Treisman, 1964), and investigations of this type have revealed the critical part played by the anterior cingulate cortex (ACC) (Pardo et al., 1990; Larsson et al.,

Fig. 7. A major part of the mammalian central nervous system is shown in this diagram, in which color aids distinction between the cerebrum (gray), BG (yellow), Cb (orange), thalamus (green), brainstem nuclei (brick red), hippocampus (turquoise), hypothalamus (light blue), amygdala (dark blue) and receptors (purple). The green and red lines represent excitatory and inhibitory routes, respectively, not individual axons. Similarly, branching of lines indicates duality of routes, not the presence of axon collaterals. The somewhat thicker black lines at the upper right indicate influence in a more general manner. The dashed lines indicate processes involving the environment. Only two representative regions of the Cb are shown, to avoid unnecessary complexity. The abbreviations are: PMA, premotor cortex; SMA, supplementary motor cortex; FEF, frontal eye field; SNpc, substantia nigra pars compacta. The abbreviations for thalamic nuclei are: LGN, lateral geniculate nucleus; MGN, medial geniculate nucleus; MD, medialis dorsalis; VAmc, ventralis anterior medialis caudalis; VApc, ventralis anterior pars principalis; VLc, ventralis lateralis caudalis; VLm, ventralis lateralis pars medialis; VLo, ventralis lateralis pars oralis; VLps, ventralis lateralis pars postrema; VMp, ventralis medialis postralis; VPLo, ventralis posterior lateralis pars oralis.

1996; Carter et al., 1998; Shima and Tanji, 1998). This component of the cerebrum is known to serve pain perception-always a possible consequence of a motor act-as well as other potential provokers of attention (Vogt et al., 1992; Rainville et al., 1997). Recent studies reported by Gehring and Knight (2000) indicate that ACC makes its contribution by detecting conflict, and that the PFC also participates in this sentinel function, in the service of response preparation. Cohen et al. (2000) have suggested, additionally, that these functions are influenced by a common brainstem neuromodulatory system, namely the noradrenergic locus coeruleus (LC). (It is worth noting, in passing, that the LC is known to be active during dreaming, a subject to which we will return below.) It has long been appreciated that novel behaviors, such as learning new skills and solving problems, involve different brain regions than those called upon in routine challenges (Shallice, 1988). Recent single-neuron studies have demonstrated that the ACC becomes active when problem solving (by macaque monkeys) involves a serial order of movements (Procyk et al., 2000). It is true that the series in question stretched over many seconds, whereas the sequences of muscular movements we have been discussing would be of shorter duration. This does not rule out that the two regimes could be linked, however.

The functional linkages (Friston, 1994; Büchel et al., 1999) set up between the motor areas and the BG, as a consequence of experience, are effectively short cuts to that clutch function mentioned above; they are records of the system's discovery of favorable and unfavorable sensory-motor scenarios. (One should note also the additional influence from the deep layers of the sensory cortex (SC)) As has already been discussed, a single motor area would be inadequate for providing *sequences* of movements, so the system shown in Fig. 7 can additionally call upon the supplementary motor (SMA-self-paced) and premotor (PMA-externally-provoked) areas. The spectrum of dendritic delay times that results when a group of axons synapses onto a group of neurons makes possible a variety of spatiotemporal patterns of output signals from the impinged-upon neurons (Mel, 1994; Nielsen, 1997), and phylogenetic or ontogenetic reinforcement will select from amongst the myriad possibilities. In the honeybee, which, as we saw above, also has a premotor area (Hammer, 1997), the reinforcement was clearly of the phylogenetic type, since honeybee behavior shows no discernable variation (Visscher and Camazine, 1999), whereas there must be considerable ontogenetic reinforcement in the nervous systems of mammals.

Spatiotemporal outputs are probably also produced by stages *prior* to the SMA and PMA, as discovered in the locust (Wehr and Laurent, 1996); specific odor molecules impinging upon the olfactory receptors in that creature lead to oscillatory signals which vary in both space and time. The setting up of such patterns in both the SC and the SMA/PMA areas could permit self-organization, the signals making several transits around the SMA/PMA-ACC-SC and SMA/PMA-ILN-SC loops (ILN being the acronymic designation for the thalamic intralaminar nuclei). The signals would be gradually modified, during successive transits, and it was suggested (Cotterill, 1997a) that this process could underlie both attention (Treue and Maunsell, 1996) and binocular rivalry (Leopold and Logothetis, 1996).

Insects like the honeybee and locust possess no counterpart of the ACC and ILN. Though there is slow feedback analogous to the left-hand dotted line in Fig. 7, as shown in Fig. 5 for the honeybee, their rapid responses appear to be exclusively of the feed-forward type, with no evidence of *conscious* cognition (Visscher and Camazine, 1999). The line of medium thickness in Fig. 7 indicates the analogous unconscious route in mammals. It is true that there are both feed-forward and reverse projection axons in the mammal (Zeki and Shipp, 1988; Singer, 1995), and there have been suggestions (Tononi et al., 1992) that the latter could actually mediate consciousness. As will be discussed later in a separate section, it seems more likely that they serve creativity.

Unprovoked input can lead to an immediate (unconscious) reflex, while alternative routes (indicated by that medium-thickness line in Fig. 7) include the short-cut which passes directly through the amygdala, without invoking cortical activity. That direct route creates movement by releasing the inhibition otherwise exercised by the BG, output from the amygdala leading to disinhibition (because the various routes through the BG involve two successive inhibitory connections, as can be seen from Fig. 7). There is also the route which follows the medium-thick line as far as the SC and then nevertheless passes to the BG, again releasing inhibition, and giving a response presumably more nuanced than that produced by the short-cut path. Finally, there is the route which penetrates as far as the SMA/PMA region. As will be discussed at length below, this *can* lead to consciousness, activating the two shorter loops referred to above and permitting them, in conjunction with the gating function of the nucleus reticularis thalami (NRT), to control attention (Merker, 1971; Crick, 1984). But all this does not *have* to happen, because the signaling may be confined to the direct, unconscious, feed-forward route indicated by that medium-thick line, the mechanism being equivalent to the one seen in honeybees and locusts.

3.2. Connections from the Cb and related regions

There is no shortage of credible models of cerebellar function (Houk, 1989; Arbib et al., 1995; Stein, 1995; Yeo and Hesslow, 1998), but let us enquire as to what

the circuitry might be supporting. The SMA/PMA dendrites would produce a spectrum of delays spanning an interval of roughly 10 ms, maximal dendritic delays being of about that magnitude. There could not be much of a motor pattern in such a narrow temporal window. But signals are perpetually in transit around the various loops, including the major one which runs through the environment. The job of the SMA/PMA is thus not to prepare several seconds of spatiotemporal patterns, that is to say several seconds of a motor sequence, but rather to set up the specific few-millisecond pattern which represents the desired response to an impinging pattern of similarly brief duration.

The thalamus comprises multiple nuclei, and no two routes from either the BG or Cb, to the motor areas, pass through the same region of the same thalamic nucleus (Asanuma et al., 1983; Jinnai et al., 1993; Anderson et al., 1993; Nakano et al., 1996; Hoover and Strick, 1999). This is true even of the caudal region of ventrolateral nucleus, VLc, because the neurons which serve the internal segment of the globus pallidus (Gpi), and the dentate nucleus (DN), lie in mutually removed parts of that nucleus (de las Heras et al., 1994; Steriade et al., 1997). We should note also the systematic connections of the two BG output regions, and the two deep cerebellar nuclei, to the motor areas. (Other deep cerebellar nuclei, serving other cerebellar regions, are not discussed here.) The GPi is connected to the SMA/PMA region and also to the primary motor cortex (M1), but *not* to the PFC. The same is true of the interpositus nucleus (IPN). Conversely, the substantia nigra pars reticulata, SNpr, is connected to the SMA/PMA and the PFC but not to M1. Similarly, the DN is linked to the SMA/PMA and the PFC. Only the DN-M1 connection fails to respect this neat distinction between routes.

What benefit could accrue from the Cb's participation, given that it can be dispensed with-though this leads to impaired coordination (Yeo et al., 1984). The synapses between the parallel fibers (ultimately fed signals by the mossy fibers) and Purkinje cells (whose dendrites receive signals from the parallel fibers and the climbing fibers) is subject to long-term depression (LTD), if the mossy fiber and climbing fiber inputs repeatedly fire in conjunction (Ito et al., 1982). This is equivalent to a slowly developing inhibition, and because the Purkinje cell outputs to DN and IPN are inhibitory, the overall effect is disinhibition. The permissive action of disinhibition is thus seen in the outputs of both the BG and Cb, the former being rapid while the latter develops slowly. Adding the similarity of the post-thalamus connections to the motor areas, we glimpse the overall strategy, those patterns of activity in the SMA/PMA will be favored which receive simultaneous input from a cerebellar output nucleus and a BG output nucleus. The situation is thus that shown schematically in Fig. 8. To a lesser extent, because they receive fewer inputs, the same is true of M1 and PFC.

Inputs to the Cb fall into several classes, one stemming from efference copy of the signals passing down the pyramidal tract, the main path leading to the muscles, which thus cannot be ordered to move without the Cb being informed (see the lower half of Fig. 7). External input, of either the fast feedback or unprovoked type, arrives via appropriate mossy fibers. Finally, other mossy fiber input originates in the SC, reaching the Cb via the pontine nucleus (Schwarz and Thier, 1999). Collectively, there is a strong implication that the Cb serves the overall mechanism by relieving it of repeating neural computations associated with oft-occurring events; it is strategically placed to inform the system of *what usually happens*, an arduous service because our routine movements give rise to a prodigious amount of 'standard' feedback (Miall, 1998; Kawato and Wolpert, 1998).

3.3. Connections from the sensory cerebrum

We turn now to the third of the routes depicted schematically in Fig. 8, namely the one emanating from the SC, that is to say from the occipital, parietal and temporal lobes. It has long been known that the major receiving regions of the frontal lobe are the premotor area (PMA) and supplementary motor area (SMA), as shown in the figure (Kertesz and Ferro, 1984). These areas pass on signals to the motor cortex (M1), and they receive from the PFC. The PFC also receives signals from the SC, as well as from the sub-cortical regions shown in Fig. 8. All of these routes are indicated in Fig. 7.

Experimental data for the monkey cortex, stemming from many different sources, have been collated by Felleman and Van Essen (1991), who produced a circuit diagram which is complex yet orderly. They positioned the various cortical areas on a hierarchical grid. The lower levels were close to the various types of sensory input, while higher echelons corresponded to association regions. Still farther up were the cortical regions of the frontal lobe. All regions were found to enter into several inter-area connections, though the multiplicity of these varied from less than ten to more than twenty. The connections in this scheme refer to routes, of course, and not to individual axons.

A noteworthy feature of these inter-area connections is that some, but not all, of them are reciprocal; some of the routes comprise axons which run in the SC-PMA direction while others run in the PMA-SC direction, for example. Each neuron in a given dispatching area sends axonal connections to many different neurons in the receiving area, of course. Zeki and Shipp (1988) discovered an interesting asymmetry in the arrangement. The spread of these connections in what could be called the forward direction (that is to say the SC-PMA direction, for example) is not as wide as the spread found in the

corresponding backward direction. The corollary is that a receiving neuron has a catchment region in a lower area of the hierarchy which is narrower than that of a neuron in the lower area receiving from the higher area. Given that such reception from many neurons permits the receiving neuron to capture correlations in the firing of the dispatching cells, one sees that the correlation-capturing facility is greater in the backward direction than it is in the forward direction.

It is important to bear in mind that reciprocity in a specific inter-area interaction refers to the route as a whole, and *not* to the individual neurons; if neuron N_1 in one area of a reciprocal pair of areas receives from neuron M_2 in the other area, it does not necessarily follow that neuron M_2 will receive from neuron N_1. Cotterill and Nielsen (1991), when seeking to explain the gamma-band oscillations discovered by Gray and Singer (1989), noted that this no-closed-loops arrangement would favor the capture of *dynamic* correlations. They showed that if the oscillations arise from interactions between different cortical areas, as opposed to interactions within a single area (Singer, 1990), maintenance of the oscillations is actually favored if these correspond to coherence in features widespread in the sensory input. (In reality, the no-closed-loops arrangement is more likely a few-closed-loops situation, but the analysis would still be valid, as long as the closed loops were in the clear minority.)

Cotterill and Nielsen also noted that learning could take place through modification of synapses serving both the forward and the backward projections. Singer (1995) subsequently emphasized that these differently-directed learning mechanisms could serve two distinct purposes, learning in the forward direction would help to tune such general functions as the orientation selectivity in the visual system, for example, while the reverse-directed learning would more likely be devoted to the specific experiences of the individual animal. We will return to Singer's important suggestion later, when considering creativity.

Felleman and Van Essen (1991) had included an account of the types of connection that are present between different layers of the cortex, both with respect to intra-area and inter-area projections. These were subsequently analyzed by Crick and Koch (1998b), who noted a complete absence of strong directed loops. This fascinating finding, which can be regarded as complementing the one invoked by Cotterill and Nielsen (1991), was rationalized by Crick and Koch on the basis that, 'a strong excitatory loop would throw the cortex into *uncontrolled* oscillations, as in epilepsy' (my italics). The fact that oscillations are observed in the cortex (Gray and Singer, 1989) naturally lends weight to this idea. Crick and Koch drew an interesting analogy when they noted, 'This was also true for early radio sets that emitted howls (caused by positive feedback) if the volume control was turned up too high'.

The Crick-Koch analysis is clearly very valuable, but one could speculate whether the absence of strong loops serves another (and possibly *additional*) purpose. The point is that if the thalamocortical system were capable of producing strong signals, unaided by the brain components discussed in the preceding two sections of this communication, sensory input might lead *unavoidably* to mucular movement; there would then be no way of controlling behavior, in the manner made possible by those other components. In fact, since there is always the major loop which closes via the environment, one could say that the Crick-Koch analogy with howling in maladjusted radio sets is indeed a valid one; the presence of strong thalamocortical loops would make every transaction with the environment a hazardous one!

The obvious alternative (or augmentative) explanation is that the lack of strong loops provides the system with several options. In the absence of sufficient supporting stimulation from the BG and the Cb, it is possible that signals in the cerebrum and the thalamus merely serve thought, rather than overt muscular movement. The actual situation would clearly require more of the anatomy than this neat division suggests because we can think and act simultaneously, and the thoughts may or may not be on the act one is performing. We must return to this central issue later, when other issues have been adequately discussed.

4. Conscious and unconscious action

There is no universally-accepted theory of consciousness (Crick and Koch, 1998a; Tononi and Edelman, 1998; Frith et al., 1999) and mystery still surrounds the function of such prominent brain components as the Cb (Bower, 1997; Middleton and Strick, 1997, 1998), hippocampus (Jarrard, 1995; O'Keefe and Burgess, 1999), amygdala (LeDoux, 1992; Swanson and Petrovich, 1998; Adolphs, 1999) and BG (Graybiel, 1995; Rothwell, 1995; Brown and Marsden, 1998). Consciousness is the most sophisticated aspect of animal behavior. When it prevails, response need not automatically follow stimulus. It appears to occupy the uppermost echelon of a hierarchy having the primitive reflex at its base, ascending levels of the hierarchy involving increasingly complicated motor responses. Carpenter (1996) argues that *every* motor response is really a reflex, and that consciousness, playing no essential role, is a mere epiphenomenon (Huxley, 1894). A rebuttal to that extreme view maintains that consciousness is required when intricate reflexes are being acquired, a stance that is being adopted here. But in the light of what emerged in our review of primitive organisms, we should challenge the placing of consciousness atop a reflex-based hierarchy.

What could be called a back-to-front theory of consciousness accords primacy to the organism's output rather than its input (Cotterill, 1998). It postulates that consciousness does not develop exclusively in the cerebral cortex's sensory-processing areas, prior to signals possibly being sent to the motor-planning areas, as Crick and Koch (1995) appear to suggest, but rather that it prevails only when those latter areas have already been activated. This communication is attempting to bolster the argument for that alternative mechanism by showing how it could have evolved, and by reviewing supportive evidence from mammalian anatomy. And the paper is arguing that this mechanism can be linked to intelligence and creativity in an attractively transparent manner.

4.1. The consciousness model

The central idea of the mechanism being advocated here concerns the influence on a currently proceeding (or currently planned) muscular act. That influence stems from motivation-triggered anticipation of the act's outcome, and it is conjectured to prevail only if consciousness is present. Because motivation relates to the self, while an act's consequences can include environmental components, consciousness is seen as lying at the operational interface between body movement and the body's surroundings. The anticipation is mediated by specific anatomical features, the independent functioning of which underlies thought-essentially simulation of the body's (sometimes passive) transactions with its milieu. Only through those anatomical attributes can a creature possess consciousness, and they are not found in all animals having nervous systems. The honeybee and the lamprey, which we discussed earlier, do not possess consciousness because their nervous systems lack certain vital components and connections.

When a child attempts its first step, prior attainment of the balanced upright position will have involved failed attempts, with attendant pain. What leads to that discomfort will have been stored as memory of possible sensory feedback resulting from certain self-paced movements. Likewise, the fact that forward motion can be achieved by specific muscular movements will already be part of a repertoire accessible unconsciously. Ultimately, the child hits upon the correct combination and timing of elemental movements and the first successful step is taken. That consolidation into a more complex motor pattern is temporarily deposited in explicit memory (Squire, 1992), and subsequently transferred to long-term implicit memory (Schacter et al., 1990), probably during the frequent periods of sleep (Stickgold, 1998) which are an infant characteristic. Soon, the toddler is able to walk without concentrating on every step, and more complicated foot-related scenarios will enjoy brief sojourns at the center of the explicit stage.

What is the precise role of consciousness in these little dramas? It supplies the vital watch-dog function during that consolidation process. The adequately endowed system conjures up a simulated probable outcome of the intended motor pattern, and vetoes it if the prognosis is adverse. The simulated outcome lies below the threshold for actual movement, and the mimicking requires two-way interaction between the nervous system and the spindles (Matthews, 1972, 1982; Proske et al., 2000) associated with the skeletal musculature, particularly when the muscles are already in the process of doing something else. The interplay provides the basis of sensation, this always being in the service of anticipation. Nausea, for example, is the sensation associated with an anticipation of vomiting (Cotterill, 1998).

Implicit memories can be drawn upon unconsciously, without demands on attention. (This point will be discussed further below.) Attention can thus be focussed on the novel task in hand. The bottleneck in sensory processing (Broadbent, 1958) arises because planning of movement is forced to avoid potential conflict between the individual muscles. Because we learn about the world only through our actual or simulated muscular movements, this was postulated to produce the unity of conscious experience (Cotterill, 1995, 1998). Intelligence then becomes a measure of the facility for consolidating elementary movements (overt or covert) into more complex motor patterns, while creativity is the capacity for probing novel consolidations.

4.2. Some revealing sentences

The previous section made a number of claims for which it did not immediately offer support. By way of underpinning the credibility of those conjectures, we will now consider some illustrative sentences. But let us first remind ourselves that a stimulus can be followed by a response after a time delay that varies over a wide range. Indeed, one could say that this range is effectively infinite; a response can be almost instantaneous, whereas at the other extreme it may never actually come, the sensory input merely giving rise to thoughts. Many would regard that latter option as obvious, because there is no obligatory involvement of muscular movement in thought processes. As a case in point, we may note that the reader of these words may be scanning my text while remaining quite motionless. Let us now attempt to demonstrate the weakness of that assumption.

We are going to start by reading a few sentences, *aloud*, even though we might be alone as we do so. And let it be stressed that these sentences are to be taken at face value; they contain no deliberate errors or other such artifice. The first sentence, taken from the realm of solid-state physics, is: NANOSCALE OXIDES ON

COPPER SURFACES HAVE THE SAME ELEC-TRONEGATIVITY AS THAT SEEN IN BULK OX-IDES. The second, more generally applicable to the scientific endeavor; is something with which we are all familiar. It is: FINISHED FILES ARE THE PRODUCT OF MONTHS OF SCIENTIFIC STUDY COMBINED WITH THE WISDOM OF YEARS. The third sentence has still wider appeal; it will be readily understandable to anyone who has traveled the countryside in the U.S.A. Here it is: THE STATE TROOPER DID NOT PERMIT US TO ENTER THE NATIONAL PARK WITHOUT A PERMIT.

We are now going to give those sentences a second reading, but this time making things somewhat more difficult. In the case of the first example, we will count up the number of times we encounter a specific letter, while reading aloud the sentence straight through from start to finish, *without repeating any sections*. And to make things as easy as possible, let us focus on the letter N because the sentence begins with that letter. Here we go: NANOSCALE OXIDES ON COPPER SURFACES HAVE THE SAME ELECTRONEGA-TIVITY AS THAT SEEN IN BULK OXIDES. Having made a mental (or written) note of our tally, we proceed directly to that second sentence, counting the number of times we encounter an F, because that is now the initial letter. Here we go: FINISHED FILES ARE THE PRODUCT OF MONTHS OF SCIEN-TIFIC STUDY COMBINED WITH THE WISDOM OF YEARS. Having made a note of that second number, we come to the third sentence again. It was: THE STATE TROOPER DID NOT PERMIT US TO EN-TER THE NATIONAL PARK WITHOUT A PERMIT.

In the case of this latter sentence, we have not counted (and made note of) letters because it has a different significance. When it is read at normal speed, there is insufficient time for individual words to enter consciousness before being pronounced. This follows from observations reported by Libet et al. (1979), which demonstrated that it takes about 500 ms for an unpro-voked stimulus to make its impression on conscious-ness. It takes about a tenth of that time, roughly 50 ms, to articulate a single phoneme. Let us enquire, there-fore, as to what happens when we read that third sentence. It was first used by Velmans (1991), when he posed the fascinating question, *Is human information processing conscious*?

The first thing to note is that the six-letter string P-E-R-M-I-T admits of different pronunciations, per-**mit** and **per**mit, though we are apparently unaware of the fact when reading the sentence. We use the correct pronunciations because of the differing contexts, of course, and it is interesting to contemplate the actual kinematics of articulation. Noting the above-mentioned 50 ms, and assuming an average of two phonemes per

syllable, we find that we have articulated twelve phonemes, contained in five *unambiguous* words, before we reach the potentially ambiguous P-E-R-M-I-T, and that about 800 ms have elapsed (allowing a parsimo-nious 50 ms gap between words). There is thus enough time for the *meaning* of the first few words to have started entering consciousness, and this enables the language system to make the correct decision when faced with the task of correctly intoning P-E-R-M-I-T.

But what do we intend to convey by that word *meaning*? Let us assume that meaning, in the context of language at least, is the province of semantics, whereas pronunciation of single words usually belongs to the realm of syntax. Moreover, let us assume that seman-tics involves the emotions while syntax does not. This leads to the conclusion that emotion-free syntax is not predicated on consciousness, given sufficient proficiency with language at least, while emotion-charged seman-tics *does* require consciousness.

That word proficiency is important. The present au-thor recalls the first time he encountered the word *inevitable*, and the mirth of his classmates when he incorrectly placed the stress on the third syllable. Even the teacher found the situation hilarious, and the au-thor's embarrassment certainly involved strong emo-tions. So in acquiring reflexes, as when learning a language, consciousness is a *sine qua non*. But once the necessary familiarity has been acquired, individual words can be articulated unconsciously, just as we can walk without concentrating on each individual step.

The reader must be wondering about those tallied Ns and Fs in the first two sentences. Let us return to them, and possibly be astonished! For it turns out that there were six Ns and six Fs. If the reader is well-versed in English, the first six should cause no surprise. But that second six may come as a shock, because the majority of people count only three Fs; we tend to overlook the F present in the word OF, which occurs three times. It might seem that they were overlooked because they appear in words of minor importance, but this explana-tion is countered by our *not* overlooking the Ns in the two words ON and IN. Our success in scoring that first six is attributable to the fact that pronunciation of all six Ns involves the same phoneme. Those three default-ing Fs, on the other hand, were missed because they were pronounced as if they were Vs. This is a profound point, and not merely an entertaining diversion. It shows that when we search for something, we have to invoke the muscular movements that would be required to characterize it. Later, we will tie this to the impor-tant issue of raw sensation, but meanwhile we may note that these ideas do not harmonize with Block's sugges-tion (Block, 1995) that there are two distinct forms of consciousness; phenomenal consciousness and access consciousness. Phenomenal consciousness and access consciousness, according to the view being presented

here, must at the deepest level draw upon one and the same mechanism.

If the reader is less than convinced by this argument, let us also note that we can repeat, upon demand, a sentence spoken by another person, but only if that sentence has been consciously attended to. This too demonstrates that we are concentrating on something only if we set up the muscular patterns that would be required to repeat it. This might seem like a waste of resources, for it suggests that we constantly make such covert preparations, without using them. One would not be able to set up and *retain* the muscular motions required to regurgitate ten minutes of another's narrative. The alternative is that the motor patterns, once set up, are retained for a few seconds (probably) and then discarded, only to be replaced by words heard more recently. This seems to be the gist of working *memory*, in the context of listened-to language. And in the related context of active language, the theory would suggest that a similar thing happens, emotion-charged semantics being the counterpart of those (consciously) attended-to phrases that we store briefly when concentrating on another person's words.

4.3. Raw sensations

Consciousness has been characterized as an awareness of one's surroundings, of one's situation, and of one's thoughts and feelings (Onions, 1962). But such definitions shed no light on the question of where this awareness is being registered. Where is one's me-ness? A strong hint comes from considering the nature of sensation.

Pain, in particular, reveals the utility of sensations, which are frequently referred to through the term *qualia* (singular, *quale*). They enable us to pinpoint something requiring attention (part of the body in this case). And phantom limb pain (Melzack, 1990) is special because it is felt in a body part which no longer exists. This suggests that a sensation felt in one part of the body must be a collective product of processes taking place in some or all of the others. How and where is the responsibility apportioned amongst those surviving members? The PMA/SMA would seem to be involved because that region has to ensure an absence of conflict between the muscles in any planned motor sequence. The impressive mirror-aided 'amputation' of a phantom limb (Ramachandran and Hirstein, 1998) was accomplished by making the patient accept as real a limb merely seen in reflection. This probably gave the BG and Cb the wherewithal to readjust the PMA/SMA's locally effective neuronal connections.

Likewise, the sensation associated with something perceived beyond the body—a red object, say—must be linked to the anticipation to react. Such anticipation requires measurement of *rate* of change. Without this capability, reliable prediction would be impossible. Only one type of component is imbued with that higher-order capacity; the sub-class of muscle spindles comprising nuclear bag fibers (Matthews, 1972). It is interesting that PMA/SMA has direct links with the spinal cord (Dum and Strick, 1991), this route paralleling the pyramidal tract. If these connections run to the spindles (via intermediate synapses, of course), as indicated in Fig. 7, they could cooperate with the route returning signals to the SC (Oscarsson and Rosén, 1963), such return being an exclusively mammalian anatomical feature.

4.4. On thinking and acting

We can think without acting, act without thinking, act while thinking about that act, and act while thinking about something else. Our acts can be composite, several muscular patterns being activated concurrently, though we appear not to be able to simultaneously maintain two streams of thought. When we think about one thing while doing something else, it is always our thoughts which are the focus of attention. This suggests that there are least two thresholds, the higher associated with overt movement and the lower with thought. Assuming that the signals underlying competing potential thoughts must race each other to a threshold (Carpenter, 1988, 1992, 1999a; Carpenter and Williams, 1995; Bundesen, 1998), it may be highly significant that cortical and thalamic projections form no strong loops (Crick and Koch, 1998b). As mentioned earlier, the presence of strong loops could make overt movement too automatic. We can now add a second possible penalty; thoughts might otherwise establish themselves by default. One should note that overt movement and mere imagery-that is, covert preparations for movement-appear to involve identical areas (Decety, 1996; Schnitzler et al., 1997; Jeannerod, 1999).

Fig. 7 (augmented by Fig. 8) indicates that the competition (Kinomura et al., 1996; Posner and Rothbart, 1998) is played out in a group of collectively functioning components, these being the sensory, motor and anterior cingulate areas of the cortex, the thalamic ILN (in conjunction with the NRT), the amygdala, and the striatum. In mammals, the latter has a heterogeneous structure (Graybiel and Ragsdale, 1978) in which the continuous matrix (M) in Fig. 7 is interdigitated with the isolated striosomes (S-here represented by a single member). The input to the S appears to be more intimately connected to the components just identified. Given that its output reaches M1, via the GPi, whereas the matrix output does not, it seems that the S may be more essentially related to consciousness. (We recall the tentative *individual* motor elements of the infant.) Likewise, the pars intermedia seems to be the more intimately consciousness-related part of the Cb, because it

has analogous projections. And the threshold for overt movement may be exceeded only when both M1-feeding components are dispatching signals concurrently. The matrix, conversely, appears to serve already-established motor patterns, because its output ultimately reaches the PMA/SMA and the prefrontal area. Its cerebellar partner is clearly the hemispherical region. It is worth noting that the cerebellar hemispheres are particularly prominent in the primates, and that they are preeminent in humans; they appear to bear much of the responsibility for making us what we are.

The focus of competition for attention appears to be the PMA/SMA, because it receives from all the thalamic nuclei handling BG/Cb output. And attention is influenced by more remote regions of the system, which feed signals to those BG/Cb components. We have already discussed the amygdala's control of the BG. The inferior olive seems to play a complementary role for the Cb, sending signals through the climbing fibers when something unexpected occurs (De Zeeuw et al., 1998) and, because LTD will not yet have had time to develop for this novel situation, disturbing the permissive effect of the disinhibition. The periodic shifting of attention, as when we simultaneously converse (or merely think) and drive in a busy thoroughfare, must make considerable demands on the putative differential clutch mechanism mentioned earlier, and this could be the dual responsibility of the substantia nigra pars compacta (SNpc) and the sub-thalamic nucleus, which appear to serve as gain controls for the striosome-related and matrix-related routes, respectively. Whence our ability to (covertly) think of one thing while overtly doing another.

Thoughts, according to this scheme, are merely simulated interactions with the environment, and their ultimate function is addition of new implicit memories, new standard routes from sensory input to permitted motor output-new optimized complex reflexes. The term *proxied movement* appears to be apposite here. For a given set of synaptic couplings between PMA/SMA and M1, a specific pattern of output signals from the former will produce a specific sequence of muscular movements. Efference copies of those output signals, dispatched through axon collaterals, will carry the full information sent to the muscles, via M1, but they will not directly produce movement because their target neurons are not immediately concerned with motor output. Those efference-copy signals may be above the threshold for thought, however, and the latter will thus be subtly tied to a pattern of motor output; whence *proxied* movement. This is the mechanism which is believed to underlie that overlooking of those Fs, in the three occurrences of the word OF.

The duality of routes, and the fact that these overlap in the PMA/SMA region, could well underlie the interplay between explicit and implicit in brain function.

That region might be the common ground where semantics dictates syntax, and where the first step of the infant invokes elemental motor fragments already learned. Given its strategic location, and its connections to other brain parts, the hippocampus is ideally placed to mediate the consolidation needed when complex reflexes are thereby acquired (see Fig. 9). According to the ideas being expressed here, it ties signals in the motor areas to the activity in the SC that results from the corresponding movement (Cohen et al., 1999). When the motor output is straightforwardly related to movement of the body within the environment, neurons in the hippocampus will appear to be place cells (O'Keefe and Nadel, 1978), but the hippocampus must serve more than mere spatial navigation (Maguire et al., 1998). It captures correlations between all motor patterns and the resulting sensory feedback. And the captured contexts are thereafter available for generalized muscular 'navigation' in a manner that could be compared with dead reckoning (Sharp, 1999).

It is possibly of significance that the circuitry in the hippocampus is not as straightforward as one might have expected. As shown in Fig. 10, the pattern of connections which link the various regions on the route from the entorhinal cortex, through the hippocampus, and back to the entorhinal cortex do not merely join adjacent regions (Deadwyler et al., 1988). On the contrary, several of the regions project not only to the next region in the sequence but also to one or two of the regions after that. The entorhinal cortex, for example, projects to the dentate gyrus, to the CA3 region, and even to the CA1 region. Likewise, CA3 projects not only to CA1 but also to the subiculum and the entorhinal cortex.

In trying to understand the reason for this complexity, it is useful to bear in mind that *N*-methyl-D-aspartate (NMDA) type glutamate receptors (Watkins and Collingridge, 1989), which are eminently suited to the capture of correlations, are profusely present in the CA1 region and reasonably well represented in CA3. The pathway between the dentate gyrus and CA3, conversely, appears to be essentially devoid of these receptors. It is also worth noting that rhythmic activity is much in evidence in the hippocampus, oscillations in the 5–12 Hz theta band being particularly prominent. The amplitude of these oscillations is highest in the CA1 region, just where the NMDA-type glutamate receptors are most dense, and it is intriguing to find that the ion channel through the NMDA receptor remains open for almost a fifth of a second (Watkins and Collingridge, 1989), that is to say about as long as the interval between adjacent theta pulses. When one recalls that a fifth of a second is also the duration usually assumed for an elemental cognitive event, one sees that the hippocampus appears to be optimized for the handling of signals intimately involved in cognitive recording.
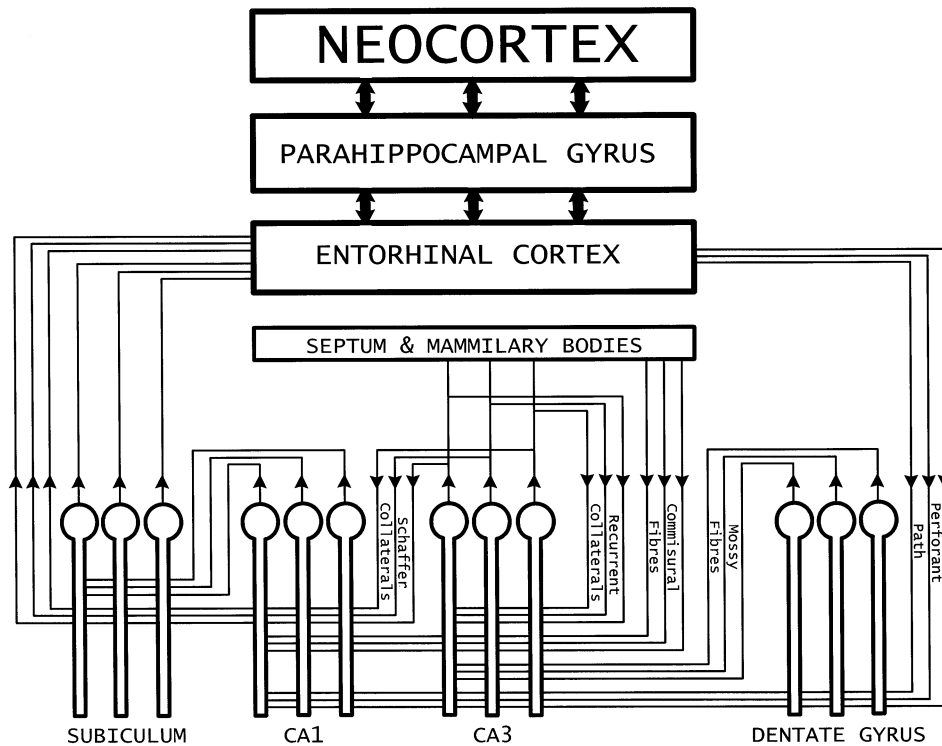
Fig. 10. This highly schematic diagram shows the positions of the main groups of neurons in the hippocampus, only three cells being shown at each location, for simplicity. The connections form a closed loop, emanating from the entorhinal cortex and ultimately returning to it. The circuit is complicated by the fact that most of the areas project to more than one other area in the sequence. It is possible that this mediates a form of integration over a brief time interval, which could serve the system by providing it with what could loosely be called a context filter.

Returning to the unusual multiple connectivity, let us analyze the instantaneous situation at a CA3 neuron, say. The transit time along an axon can be ignored because action potential transmission is rapid and the axonal segments in question are rather short. The delays will thus be almost exclusively due to the far more sluggish transits along the dendrites, such transits amounting to some 10 ms. The CA3 neuron will be receiving signals simultaneously from the entorhinal cortex and from the dentate gyrus. The signals from the entorhinal cortex will have been dispatched from that region *immediately* prior to their arrival at the CA3 neuron, whereas the signals from the dentate gyrus will be related to signals dispatched from the entorhinal cortex as much as 10 ms *previously*. This means that the CA3 neuron is integrating over time as well as over space (the space factor deriving from the fact that the CA3 neuron receives from many neurons in each of the other two implicated areas). The temporal integration is even more extensive in the case of a CA1 neuron, because the multiplicty of the reception is even greater in that area (see Fig. 10).

These integrations are nevertheless not being carried out over a time scale as long as the fifth of a second between theta pulses, let alone the half second that Libet and his colleagues demonstrated is required for conscious awareness (Libet et al., 1979). They are remi-

niscent of another time scale, however, namely that of the typical phoneme. (This would be true especially of the integration performed by neurons in the CA1 region.) It could be that the integrations ensure that only signals related to muscular events having at least this duration will be able to penetrate through the hippocampal circuit, and become candidates for contributing to the storage of relevant correlations. One could call this mechanism a dual relevance filter and temporal binder.

4.5. When and why is consciousness essential?

A major problem confronting those who would explain consciousness is its apparently multifarious nature; there seems to be too large an inventory of its advantages to permit a succinct definition. The present article attaches great significance to its provision of new context-specific reflexes, as occurs when one is learning to walk or acquire proficiency with language. But others would give higher priority to the power of reasoning. That faculty surely requires consciousness awareness, and some might argue that reflex acquisition actually makes lesser demands. It would be a considerable breakthrough, therefore, if it were demonstrated that reflex acquisition and reasoning, and perhaps also other benefits of consciousness, are necessarily tied to

the same underlying mechanism. That ambitious goal is the subject of the present section.

Let us start by concentrating on reflex acquisition, and state clearly what is intended by that qualifier *context-specific*. It must convey more than mere association, because lowly creatures such as *Aplysia* associate, and they are not conscious. The context in question has perforce a temporal dimension, for it must relate to a *sequence* of muscular movements. This, after all, is the essence of motor patterns such as those involved in locomotion and articulation, which members of our species cannot accomplish at birth. Context specificity was clearly involved when we correctly pronounced the six-letter string P-E-R-M-I-T each time it occurred in that sentence used by Velmans (1991), as discussed in a previous section. In each case, the lead words gave the cue for the correct succession of phonemes and emphases, but only because we are adept at using English. In that previous section in which we encountered Velmans's sentence, the discussion was couched in terms of semantics and syntax. The difference between those two concepts can be generalized to include locomotion and, indeed, all things achievable through muscular movement, for one could say that semantics is to ends as syntax is to means. When a child is attempting that first step, the end is the getting from A to B, while the means is the placing of a foot in front of the body and the gradual shifting forward of the center of gravity. And when a child is attempting the first meaningful vocalization, the end is emulation of a succession of sounds which the nervous system is suggesting should be profitable, while the means is movement of muscles involved in articulation.

Functional brain imaging has recently been producing information regarding the brain regions that are active during the use of language, and the technique has provided evidence of a distinction between semantics and syntax. Whereas use of the latter involves activation of Brodmann's area 44 (the pars opercularis of the frontal gyrus), semantics is found to involve Brodmann's area 47 (the inferior frontal gyrus) (Vandeberghe et al., 1996; Hagoort et al., 1999; Posner and Abdullaev, 1999; Dapretto and Bookheimer, 1999). It is interesting to note, in addition, that Brodmann's area 46, which is contiguous to both area 44 and area 47, has been shown to be involved in the short-term memory of verbal information (Schumacher et al., 1996). Broca's area (Brodmann area 45), damage to which produces impairment in the actual articulation of words, is located within the triangle formed by those other three areas, 44, 46 and 47. In terms of the anatomical features discussed in the present communication, area 44 can loosely be regarded as a premotor area that serves articulation, while areas 46 and 47 play analogous prefrontal roles.

Before continuing our discussion, it should be stressed that there is a difference between saying that a particular brain region is essential to consciousness and suggesting that it is needed for the optimal exploitation of consciousness. The famous accident to Phineas Gage (Harlow, 1868) demonstrated that a large expanse of the PFC is not essential to consciousness, and the equally renowned cases of anonymous hippocampus patients, H.M and R.B, (Squire, 1987) show that the hippocampus can likewise be dispensed with. As noted above, the Cb is also non-essential to consciousness, and patients who have been subjected to bilateral cingulotomies for the relief of chronic pain (Lane et al., 1997) likewise retain possession of consciousness. But loss of any of these brain components leads to a conscious state that is severely dysfunctional in one or another respect. It is important that this be emphasized because such cases might otherwise be taken to undermine the ideas being expressed here.

The discovery that there is a common semantic system for words and pictures (Vandeberghe et al., 1996) lends support to the above-suggested generalization regarding semantics and syntax. And it is tempting to make the even more sweeping assumption that the premotor and supplementary motor areas serve means as the prefrontal region serves ends. In this same vein of rationalization, one could then ask what the prefrontal region does for the system, given that the premotor and supplementary motor regions set up motor sequences. The logical answer appears to be that it sets up a *sequence* of sequences, as when a sequence of words comprises a sequence of sequences of phonemes. This simplification would be of obvious importance if it were proved to be valid, so let us see whether it can pass muster. The discussion will inevitably involve us in a number of side issues.

The question of how the brain encodes serial order is a famous one (Lashley, 1950), and the current consensus is that this is handled by a distributed network which collectively encodes, stores and recalls the sequence (Goldman-Rakic et al., 1992; Houk and Wise, 1995). The dorsolateral PFC is a prominent component of that network, and it has been shown to make its contribution by selecting actions on the basis of serial order (Milner et al., 1985). That the network is indeed distributed is attested to by the recent finding that even the motor cortex itself is selective for serial order (Carpenter et al., 1999), and that it is thus not simply an 'upper motor neuron'. Further evidence supporting a general rather than a specific limited mechanism is provided by investigations of the interplay between the amygdala and the PFC (Gaffan et al., 1993; Schoenbaum et al., 1998), because it has been found that the amygdala is important not only for acquisition of nondeclarative conditioned responses but also for the encoding of declarative memories (Adolphs, 1999).

Perhaps the strongest endorsement of the generality of the PFC's role comes from the sheer variety of functions with which it has been experimentally linked. That the somewhat nebulous idea of the mind's blackboard (Just and Carpenter, 1992) requires updating is seen from the fact that the PFC has now been tied to episodic encoding processes, episodic memory retrieval, long-term recognition memory for faces, mnemonic processing, semantic coding, spatial processing, sustained attention to sensory input, verbal fluency, willed word generation, word production and general working memory. Grafman et al. (1995), who compiled that list from numerous published sources, have made the useful suggestion that the PFC supports 'a cognitive architecture based on a unit of memory we have called the structured event complex (a generic knowledge structure underlying story understanding, script generation, schemas, etc.)'.

Given that Grafman et al. (1995) were using a view of cognition that has perhaps been superseded by the present communication, they cannot be criticized for failing to perceive the underlying simplicity of the situation. For their 'structured event complex' and the above-expressed idea of 'sequences of motor sequences' might be essentially the same thing. Their invoking of the word *schema* (plural, schemata) deserves comment, because that is the concept which could provide the desired clarification. Neisser's (1976) definition was:

A schema is that portion of the entire perceptual cycle which is internal to the perceiver, modifiable by experience, and somehow specific to what is being perceived. The schema accepts information as it becomes available at sensory surfaces and is changed by that information; it directs movements and exploratory activities that make more information available, by which it is further modified. From the biological point of view, a schema is part of the nervous system. It is some active array of physiological structures and process, not a center in the brain, but an entire system that includes receptors and afferents and feed-forward units and efferents.

One aspect of this definition is unfortunate. The phrase 'part of the nervous system' appears to indicate that individual schemata are embodied in specific neural circuits; they are more likely stored in the distributed and superimposed manner typical of memories in general.

The present author (Cotterill, 1997a, 1998) has suggested as an alternative:

A schema is a reproducible coactivation of neurons linking a specific pattern of motor-planning activity in the premotor area to relevant activity in the sensory areas, the reproducibility stemming from the fact that schemata are laid down in memory.

-the aim being both to put schemata on a more secure neuronal footing and to salvage as much generality as possible. Such generality is indeed achieved because one sees that even the honeybee can be accorded schemata through this definition (see Fig. 5). And mention of the honeybee serves as a timely reminder that activation of schemata is not the exclusive province of consciousness. In fact, if the definition is not limited to processes mediated by neurons, it can even be applied to the bacterium, albeit in a rather impoverished form. The bacterium's schemata are just two-fold; depending upon how much nutrient it has absorbed in the most recent few seconds, its flagellum twirls clockwise or anti-clockwise. By thus returning to the lowly bacterium, we remind ourselves that schemata and cognition are inextricably tied to each other as well as to movement. And although consciousness need not be involved, we are also reminded that a creature *knows* with its body. Cognition involves the monitoring of the body by the body, and the process is particularly efficient when it can call upon the services of a nervous system.

Mention of the bacterium suggests that the definition of a schema ought to be widened so as not to require specific involvement of sensory areas, which the bacterium does not possess. A new alternative could be:

A schema is a reproducible linking of motor-directing activity to the optimal environmental feedback resulting from that activity, the reproducibility stemming from the fact that schemata are laid down in the available form of memory.

The available form of memory in the bacterium being a primitive one, as discussed above. This definition reminds us that schemata can be called into play by purely internal events and conditions, as when hunger provokes foraging. The hypothalamus clearly calls schemata into play in such cases. Some schemata are no doubt inherited, and there is the possibility that some can be acquired by happenstance.

But where is the connection to consciousness? It will now be suggested that the schema and the quale (which, it will be recalled, are the individual elements of schemata and qualia, respectively) are related by the expression:

SCHEMA*ATTENTION→QUALE

An arrow has been used here, rather than an equals sign, because the expression is not intended to be a mathematical equation. The arrow may be taken to indicate 'leads to'. For much the same reason, an asterisk has been favored rather than a multiplication sign, and it can be taken to designate 'when accompanied by'. So, this definition has it that a schema, when accompanied by attention, leads to a quale, that is to say an element of sensation. When attention is absent, there is no sensation.

There is still something lacking from this analysis, however, because we need to specify what we mean by attention. To begin with, let us stress that given the importance being attached to motor output, it would be almost bizarre to accept that attention could be passive. Yet passivity of attention is a not unlikely consequence of theories which see consciousness as arising solely in the SC, such as those espoused by Crick and Koch (1995) and Zeki and Bartels (1999). According to the theory being advocated here, therefore, an important attribute of attention must be its essentially active character.

Could one not define attention even in the bacterium, however? As discussed in the second section of this communication, the direction of rotation of its flagellum is determined by the relative concentrations of certain chemical species. Would it not be valid to claim that those concentrations were exercising attention, at the place where their magnitudes are most critical? Attention could indeed be defined in this manner, for the bacterium, but it would have no connection with the creature's recent history other than that the latter determines the *instantaneous* magnitudes of the various molecular concentrations. No chemical record is kept of the magnitudes of the various concentrations at different times. Had this been the case, the bacterium might have been able to avail itself more directly of the information in its environment concerning the spatial distribution of nutrients. As it is, that information is merely lumped into a single number, and the bacterium's cognitive repertoire is telescoped into a single binary choice, clockwise or anti-clockwise rotation of the flagellum.

The type of attention required for acquisition of context-specific reflexes has to be much more sophisticated. And this brings us to an important word *navigation*. The navigation referred to here is more than mere locomotion through the local terrain. It is intended to be interpreted in the more general sense of exploration of what could be called muscular hyperspace, which is to say all possible combinations of muscular movements, both with respect to direction and speed (Cotterill, 1997b, 1998). And it is important to bear in mind that these muscular movements are not confined to a bacterium-like binary choice; they are continuous, both with respect to those spatial and temporal parameters. Putting it simply, one could say that there can be no context-specific reflexes if there is no record of context.

It would be easy to underestimate the profound difference between binary operation and continuous operation of a motor system. If meaningful adjustments are to be made of muscle movement and muscle acceleration, it is mandatory that the system be informed of the current values of those variables. Putting it in mathematical terms, the optimal continuation of the trajectory through muscular hyperspace demands infor-

mation about the recent path of that trajectory. And the apprising of the system of such information is, in fact, consciousness. This ties the current sensory input to the immediately prior muscular movements through which the animal probes its environment, such probing being directed by the sequence of movements dictated by the premotor and supplementary motor cortices. This is precisely what was said to provide the basis of sensation, in Section 4.2 above, so navigation in the sense being used here requires sensation, that is to say consciousness.

But what is being reported to? And what is the underlying neuronal mechanism? The answer to the first of these questions has to be the body itself, and the mechanism just as certainly must involve the interfacing of the body with the nervous system, in the service of supplying the body with information regarding the current state of, and the current changes of, the body's musculature. This brings us back to the muscle spindles (Matthews, 1972; Goodwin et al., 1972). It is well established that they keep the system informed in the required manner (Lethin, 1977; Matthews, 1982).

Let us now return to Fig. 7, the key illustration of the present communication, and note certain features that are not seen in the neural circuitry of the honeybee (Fig. 5), for example. For a start, the PMA is seen to be more special than was the case for the honeybee because it sends signals not only to the motor cortex but also back toward the SC, by way of axon collaterals. There are three such *efference copy* routes, in fact, though they ultimately all lead back to the SC. One goes directly, another passes through the anterior cingulate, and the third goes via the thalamic ILN. Another feature seen only in mammals is the intricate structure that mediates interaction between the anterior cingulate, the NRT and the ILN (Cornwall et al., 1990; Lozsádi, 1994; Groenewegen and Berendse, 1994). This part of the brain's circuitry is well suited to the control of attention (Merker, 1971; Crick, 1984; Purpura and Schiff, 1997). Finally, there are the routes through which signals are dispatched to the thalamic ILN from the spindles and other proprioceptive receptors, and to the anterior cingulate from the pain receptors. It is these routes which keep the system apprised in the manner discussed above.

But how does it all actually work? How does consciousness emerge from all this anatomy and physiology? We can now reap the benefit of all the ground-work on cognition, carried out in the early part of this communication, the key point being that cognition is inextricably tied to the body's motor apparatus. The bacterium knows with its flagellum, albeit unconsciously, because the flagellum is its only means of achieving anything. Likewise, we know with our muscles, because they are all we have at our disposal, in the quest of satisfying our needs. And because we have a

nervous system, the cognition is particularly rapid. But we have something else, in addition, namely *circuitry which enables us to know that we know*. And that higher order of knowing must, perforce, also be accomplished by the muscles.

Consciousness, then, is knowing that one knows, and this is why it is able to mediate the familiar thought processes which are commonly taken to characterize the phenomenon. In the modern human being, those thought processes are strongly influenced by the cultural environment, and are dependent upon the ability of the individual to draw upon such sources. That ability is measured by the individual's intelligence, which is the subject of the next section. Meanwhile, let us remind ourselves that human culture has developed considerably since the most recent evolutionary change, at the genetic level, so we must look for a more fundamental reason why consciousness was selected for. As has been argued above, that fundamental advantage was the acquisition of new context-specific reflexes, a mechanism which we have seen also requires consciousness.

5. Intelligence

The premotor and supplementary motor cotices are essentially the higher counterparts of the pattern generators located in the spinal cord, the classic example of which are those found in the lamprey (Grillner et al., 1989, 1995). The difference is that although a variety of motor patterns can be generated by the latter, the available repertoire cannot be altered. The patterns generated by the PMA/SMA, on the other hand, show far greater sophistication, and they *can* be reprogrammed (see Berthier et al., 1993, for related ideas). (The coordinated movements of antagonistic sets of muscles are a case in point, and their programming probably involves the Cb.)

It is this latter fact which suggests a simple definition of intelligence. *Intelligence is the ability to consolidate already-learned motor patterns into more complex composites*, *such consolidation sometimes being merely covert*, *rather than overt*. This definition was discussed in the context of autism (Cotterill, 1998), and the prediction that autistic children would encounter difficulties in executing and learning motor sequences was subsequently confirmed (Teitelbaum et al., 1998). A normal child, lying on its back and wanting to roll over onto its front, soon learns that this can be readily accomplished if first the head, then the shoulders, and finally the hips are swiveled in the same direction. If the timing of this sequence is correct, the supine-prone transition requires a minimum of effort. Autistic infants appear to experience considerable difficulty in learning this simple motor sequence. Indeed, the sequence does

not even occur in their failed attempts. Instead, they awkwardly arch their backs and ultimately fall into the desired position.

The unavoidable participation of proxied muscular movements in mental activity, being advocated in the present model, might resolve the controversy over whether the Cb is or is not involved in cognition (Leiner et al., 1986; Bracke-Tolkmitt et al., 1989; Decety et al., 1990; Wallesch and Horn, 1990; Ivry and Baldo, 1992; Ito, 1993; Schmahmann and Sherman, 1998). According to the ideas expressed being here, the Cb, when it is intact, *has* to be involved in cognition.

In general, when a new motor pattern is being acquired, both the means and the ends will be coded in currently active patterns of neuronal signals. And there must be interactions between these patterns because the goal will influence the route through muscular hyperspace by which it is to be achieved. This, after all, is what is implied by the use of the term schema. The signaling pattern related to the goal will have to persist for a longer time than that related to elemental schemata, because it has to provide the necessary continuity. In the now-standard terminology, there must be a *working memory* (Baddeley and Hitch, 1974), and there is abundant evidence that this implicates the PFC (see, for example, Funahashi et al., 1989; Goldman-Rakic, 1992; Rypma and D'Esposito, 2000). As we have seen, the PFC probably dictates *sequences* of elementary muscular sequences, but it must be borne in mind that the sophistication of the latter will depend upon what the individual has already learned. A ballet dancer would regard as an elementary motor pattern a muscular sequence which the novice would find quite difficult.

The circuitry depicted in Fig. 7 indicates how the mechanism might function. The DN and SNpr both feed signals not only to the SMA/PMA region, but also to the PFC, and there is a route from the latter to the former. Now the persistence time for signals in the PFC is longer than it is for the SMA/PMA (Birbaumer et al., 1990; Fuster, 1985), so the former area seems ideally suited to the dual job of dictating the sequence of sequences and of providing the necessary temporal continuity (Shadmehr and Holcomb, 1997). As was mentioned above, the system's ability to simultaneously handle both means and ends, *in a context-specific manner*, may depend upon that matrix/striosome heterogeneity in the striatum. This idea appears to be consistent with the detailed mechanisms proposed by Berns and Sejnowski (1996) and Doya (1999), which showed how the individual components of the BG might cooperate. Indeed, the analysis of Berns and Sejnowski was directed toward *sequences* of movements.

With sufficient experience, schemata become permanently laid down in memory, and even sequences of muscular sequences become second nature. The cliché is

the manifestation of such consolidation in the language domain. It is a noteworthy feature of the underlying anatomy, shown in Fig. 7, that it includes direct connections between the SC and the PFC. And the Cb's contribution to such ingrained behavior appears similarly to be served by the direct route connecting the SC to the Cb, via the pontine nucleus. In the case of the former route, the hippocampus is ideally situated to record the correlations between the sequencing signals dispatched to the muscles and the resulting temporally patterned feedback from the environment, because of its widespread reciprocal connections with virtually the entire cerebrum except the motor cortex (Squire et al., 1989). It is in this sense that the adjective *context-specific* is being used here, rather than in the more limited sense of background clues. But there might not be a sharp distinction between these connotations because even the information stemming from the background will often not be unvarying, because of the animal's own movements.

In any event, there is evidence that the hippocampus is implicated in context-dependent memory processing (Selden et al., 1991; Honey and Good, 1993; Young et al., 1994). In view of the recent findings of Stickgold (1998), it seems likely that the consolidation process is one of the main processes accomplished by sleep, both of the rapid eye movement (REM) and non-REM types. An important aspect of this consolidation will be the detection of novelty, because only novel correlations need be candidates for memorizing. The views that have been expressed here would lead us to expect that the premotor and supplementary motor areas, the anterior cingulate, and possibly also the PFC would all be involved in novelty detection, and this is indeed what is observed (Tulving et al., 1994; Berns et al., 1997). As the latter authors note; 'Our findings are consistent with the view that dorsolateral PFC is involved in the active maintenance of context information used for prediction, and that the ventral striatum monitors the reliability of such predictions, becoming activated when these are violated by stimuli that appear in an unexpected context'. Recall of a recently experienced novel correlation is found to require, in addition, participation of the globus pallidus, thalamus and cerebellum (Cabeza et al., 1997). It has even been found that the hippocampus itself contributes to the detection of novelty (Knight, 1996).

6. Creativity

Mere proficiency with the above-discussed consolidation process does not, of itself, guarantee that an individual will be able to invent novel solutions. Intelligence, of the relevant type, might be a prerequisite for creativity, but it is not sufficient. Carpenter's ingenious race-to-threshold mechanism (Carpenter, 1988, 1992, 1997, 1999a) has received definitive experimental endorsement (Carpenter and Williams, 1995). And his equally insightful ideas about the randomization of behavior (Carpenter 1999b) appear to hold what might be a vital clue to the neuronal mechanism underlying creativity. But that mechanism will produce only familiar winners, in the absence of new runners. Such fresh contenders might be the product of unexpected correlations being captured by those areas involved in the detection of novelty, discussed in the preceding section. And the correlations could then be returned by the feedback connections shown in Fig. 7 (Singer, 1995). Indeed, the cause of novelty might be particularly well served by the fact that those feedback connections achieve a wider spread than their feed-forward counterparts (Zeki and Shipp, 1988).

If this scenario proves to be reliable, it would indicate that an individual's anatomical endowment, with respect to the actual spread of connections between areas, is a vital ingredient in creativity. It would indicate that a creative mind is something that one is born with, though the fact that synapses continue to be formed during an infant's first two years also indicates that richness of experience at that tender age can be a contributory factor.

The question arises as to the venue for this putative race, and Fig. 7 strongly suggests that the competing signals impinge upon the premotor and supplementary motor areas, and probably also on the PFC. The race's judge is probably the amygdala, given its control of access to the BG, and the competition must also be influenced by attention, which would involve the anterior cingulate, the NRT and the thalamic ILN.

7. Further ramifications

If the views expressed in the previous sections of this communication prove tenable, they would have an important bearing on a number of related phenomena. These were not included in the main discussion because that would have made the latter cumbersome. Instead, therefore, they will be discussed in a number of individual subsections. The first topic is related to the neural underpinnings of conscious processes, while the following three items all have a bearing on the central issue of sensation. The final subsection is devoted to a discussion of the fascinating finding that certain neurons in the frontal lobe display activity when the animal is observing the motor patterns of *other* animals.

7.1. Cortical oscillations

The discovery of gamma-band oscillations in the cerebral cortex by Gray and Singer (1989) continues to

provoke debate (Engel et al., 1999a,b; Gold, 1999; Hardcastle, 1999; Newman and Grace, 1999; Revonsuo, 1999). The idea that such oscillations, and the synchrony they imply, could play a role in cognition had been anticipated by various authors (Delage, 1919; Milner, 1974; Von der Malsburg, 1981, 1997), and supporting evidence has recently been reported (Tallon-Baudry et al., 1997; Miltner et al., 1999; Rodriguez et al., 1999). For our discussion here, interest naturally focuses on whether components other than the cerebrum can be shown to support such oscillations. The present theory would seem to require that this be so. It is thus interesting to note that gamma-band oscillations have been observed in thalamic ILN (Barth and MacDonald, 1996). Steriade (1996) even went so far as to suggest that these nuclei actually coordinate the oscillations (but not *drive* them).

Given the pivotal role being envisaged for the premotor and supplementary motor areas, in the present communication, they ought also to be candidates for the task of coordination. Indeed, they could additionally provide the drive. The point is that these areas are the source of the efference copy signals which are conjectured to maintain the activity of selected neurons in the sensory areas, those copies passing directly to the sensory areas by one route and indirectly by the route which passes through the thalamic ILN. If this idea is correct, the binding conjectured to be mediated by the oscillations (Engel et al., 1999a) would be a natural consequence, and higher order binding, such as that which integrates information garnered through different senses (Frost, 1999; Dalton et al., 2000), would also be readily explained.

The ideas expressed here also draw strength from the fact that the motor areas are found to drive muscle discharge in the low gamma band (and also in the beta band). As Brown (2000) has noted; 'Synchronization in the gamma band may provide a means of binding together those particular, often spatially distributed, cortical elements involved in movement execution under conditions that vary from moment to moment and require some attention'. It could be productive if those monitoring gamma-band oscillations were to include the premotor and supplementary motor areas in their investigations. If such oscillations are indeed detected in those areas, a check should be made on possible phase locking with the oscillations observed elsewhere in the cortex.

7.2. Phantom limb sensations

A recent study of patients with missing limbs (Davis et al., 1998), in which microelectrodes were positioned in the somatosensory thalamus, has demonstrated that thalamic representation of the amputated limb remains functional. As Kaas (1998) noted, this indicates that there had been neuronal reorganization such that the territory in the thalamus corresponding to the missing limb had become responsive to the sensory inputs from the stump of the limb, whereas activation of that thalamic territory continued to signal sensations from the missing body part. He concluded that this indicates subcortical reorganization following amputation.

Franz and Ramachandran (1998) have demonstrated that the presence of a phantom limb is taken into account by the rest of the body, during behavior, and concluded that spatial properties of movement remain intact long after their associated peripheral effects have disappeared. They also found that spatial coupling is manifest only during the subjective experience of movement. Finally, they noted that learning-induced changes are the consequence of mismatch between different sources of movement-related sensory information (which is to say, feedback). The spectacular 'amputation' of a phantom limb (Ramachandran and Hirstein, 1998), referred to earlier in the present communication, is a special case of those same principles.

Phantom limbs have traditionally been explained on the basis of phenomenal persistence of body parts following deafferentation, but as Brugger et al. (2000) have noted, this is incompatible with the occurrence of similar sensations experienced by people with congenitally absent limbs. Brugger et al. studied a university-educated woman born without forearms and legs who nevertheless had phantom sensations in these missing body parts. Functional magnetic resonance imaging (MRI) revealed no activation of the sensorimotor area, but activity *was* detected in the premotor area (as well as the parietal cortex). Transcranial magnetic stimulation of the sensorimotor cortex produced phantom sensations, as did similar stimulation of the premotor and parietal areas.

These observations indicate that body parts that have never developed can nevertheless be represented in the sensory and motor areas. And the prominence of the premotor area, in particular, tends to endorse the importance being attached to it here, in connection with the experience of raw sensation.

7.3. Amyotrophic lateral sclerosis (ALS)

It is important to consider whether sensations would still be experienced even when the PMA is out of action. In the case of ALS, the disease appears to involve atrophy of the PMA but sensation seems to survive. Regarding the clinical evidence, Comi et al. (1999) have noted that neuroimaging data remain 'quite controversial'. A computed tomography (CT) study (Poloni et al., 1982) found cortical atrophy in 64% of ALS patients, and in only 12% of controls. The same technique revealed no evidence of more pronounced atrophy in ALS patients than in normal controls (Gal-

lassi et al., 1989). An MRI study found evidence of atrophy in all eight ALS patients examined (Pringle et al., 1992), while two more recent studies (Ishikawa et al., 1993; Cheung et al., 1995) failed to reveal such evidence. It is particularly noteworthy that a longitudinal study (Abe et al., 1993, 1997) is demonstrating that there is frontal lobe atrophy only in those ALS cases in which there is also dementia. The situation is not as clear-cut as one could wish, therefore, and such investigations will have to become much more specific and discriminating before they can make a meaningful contribution to the debate.

7.4. The difficulty of self-tickling

As noted earlier in this communication, a key issue in the debate about consciousness asks, *what is being reported to?* It is difficult to understand how sensation could arise from the mere confluence of neural signals, irrespective of whether these come together at a specific brain location or simply flow around one or more circuits. It is possible that insight can be gained from the phenomenon of tickling (Cotterill, 1996). Few would deny that it involves sensation, but what is this, and how does it arise?

Wieskrantz et al. (1971) studied the phenomenon with a device which gently provoked the sole of the foot, this being controlled by the subject, by another person unaided, or by another person with the subject's hand passively following the other person's movements. Different intensities of sensation were experienced, the greatest being created by the unaided other person. The conclusion was that efference copy reduces the sensation by informing the subject of what is coming, and thus by undermining the surprise factor.

Speculating about a possible role for efference copy in consciousness (Cotterill, 1995), the present author had been intrigued by the suggestion (Miall et al., 1993) that the Cb might act as a special type of predictor. In essence, this theory postullated that the system would be able to anticipate the result of moving a limb, while the limb is actually being moved. Any circuit which makes consciousness possible might need to be trained for the job, in order to permit anticipation of the sensory consequences of muscular movements. The predictor discussed by Miall et al. (1993) might serve this purpose in a particularly efficient manner (even though it was clear that consciousness does not actually require the Cb to be intact).

If raw sensation is related to anticipation of the need to move (Cotterill, 1998), the difficulty of self-imposed tickling might stem from the purported predictive capacities of the Cb (Cotterill, 1996). Blakemore et al. (1998) carried out an experiment in which brain activity was monitored by functional MRI, while tickling was in progress, and they did indeed demonstrate participa-

tion of the Cb. There was a bonus, in fact, because they also demonstrated participation of the anterior cingulate, just as the model advocated in the present communication would suggest.

Darwin (1873) published an analysis in which he noted that a prerequisite for susceptibility to tickling is that the body region in question must not be one normally receiving tactile stimulation. We seldom touch the soles of our feet, and they are ticklish; we frequently touch our own arm-pits, when washing, and they are not ticklish. Miall (1998) suggested that the Cb 'informs' the system of 'what usually happens' when we move our limbs, thereby sparing the system of keeping track of the huge amount of routine (and thus uninteresting) sensory feedback that arises as a consequence of limb movement. Fig. 7 of the present communication shows how this function would contribute to the overall scheme of things.

The really important issue concerns what this might be revealing about raw sensation. It endorses the conjectured link between sensation and the anticipation of the need to move. Nausea, for example, which seems to be a rather nebulous sensation, is seen to be nothing more than the anticipation of vomiting, which of course involves violent muscle spasms (Cotterill, 1998), as does tickling. These tickling experiments remind us that the ultimate target of the sensation-mediating nerve signals must be the body itself.

There ultimately *has* to be a monitoring of the body's current state, and the only things capable of doing this are the appropriate body components. In the bacterium, it is the flagellum. In animals like us, it must be the muscles, and probably their associated spindles. Consciousness arises from the monitoring *of* the body *by* the body, in the service of enabling the body to react in the most favorable manner, under the prevailing circumstances in the environment, and within its own self. Thinking is a bodily function.

7.5. Mirror neurons

A particularly strong endorsement of the ideas advocated here is provided by work on so-called *mirror neurons*, these being a class of visuomotor cells discovered in the ventral PMA in monkeys. These neurons become active when a specific action is performed by the animal, and also when the animal observes the same action being executed by another animal (Gallese et al., 1996; Rizzolatti et al., 1996a; Rizzolatti and Fadiga, 1998; Gallese and Goldman, 1998). There is experimental evidence which suggests that a similar action-matching mechanism operates in humans (Rizzolatti et al., 1996b; Grafton et al., 1996).

These experiments expose the specificity of planned actions. For example, some mirror neurons increase their firing rates when the monkey is grasping a morsel

of food, such as a raisin, and also when the animal watches a person doing the same thing. But the neurons do *not* react when the monkey merely observes the raisin, and neither do they respond to the animal's act of grasping in the absence of the raisin, nor to the sight of a person doing the same thing. The activation of a mirror neuron therefore contributes to the matching of observed movements to their actual execution.

This is just what would be expected if the ideas championed in the present communication are tenable. There is a fairly clear connection with that sentence-scanning exercise we performed in Section 4.2 above; those three Fs were missed because the system had already translated them into the (articulatory) muscle movements that it would have needed to make in order to intone the sound of a V. The connection between mirror neurons and language has indeed been emphasized by Rizzolatti and Arbib (1998).

There is also a connection with observations reported by Watanabe (1996), who has recorded from single neurons in the forebrain as the subject performed a delayed-reward task. He found that some cells fire selectively in anticipation of a particular type of reward, whereas others are selective for the reward's location. A third group of neurons discriminated between whether a reward had previously been seen or merely inferred through prior experience. Jennings (1996), commenting on these observations, noted that, 'the combined activity of many such neurons could in principle encode a detailed description of the expected reward, which could then be used to control goal-directed behavior'. Both these and the mirror-neuron experiments could be interpreted in terms of schemata.

8. Concluding remarks and summary

Several years ago, Middleton and Strick (1994) published anatomical evidence which suggested a possible role for the BG and the Cb in higher brain processes. As they noted at the time; 'The possibility that neurons in the BG and Cb innervate areas of the cerebral cortex that are involved in cognitive function has been a controversial subject'. The controversy was hardly surprising, given that the stimulus-response paradigm for cognition enjoyed wide support, as it still does today. These authors had discovered, in the primate, axons which connect both the BG and the Cb to the PFC. The latter is known to serve working memory, which undeniably contributes to mental processes, and hence their conclusion. But the accepted wisdom at that time placed responsibility for thought in the sensory areas, the motor areas being regarded as mere recipients of the product of those prior cognitive processes. As has been noted in the present communication, many would still regard this scenario as self-evident.

A case in point is seen in the admirable attempt by Baev (1997) to rationalize the highest forms of brain function. He devised a hierarchical scheme in which each level functioned as a discrete unit. Each unit was seen as carrying out its task in an essentially independent manner, and it comprised both a model for optimal performance, stored in memory, and a controller. Baev referred to the individual learning systems as *automatisms*, and he argued that the various members all performed according to the same functional principles.

The present communication has put forward a quite different scheme. It postulates that there is really only one unit in the brain, and that its ultimate focus is the primary motor area. All the other components are seen as feeding signals toward that motor area in a conditional manner, which is to say that they achieve this goal only if certain local prerequisites are currently being satisfied. In default of that, the signals can achieve the lower strength needed to mediate simulation of the body's transactions with the environment. Such simulations draw on stored memories of past experiences, in which the relevant stimulus was the animal's own muscular movements and the relevant response was the resulting feedback from the environment.

The simulations referred to here are thoughts, and the underlying mechanism centers on the premotor and supplementary motor areas, rather than on the primary motor area, though there is experimental evidence that the latter may nevertheless also be involved (Jeannerod, 1999). The premotor and supplementary motor areas were envisaged as being important for two reasons. First, they set up *sequences* of motor actions, in contrast to the individual muscular movements mediated by the primary motor area. Second, they are the source of efferent copy signals, these being projected back to the sensory areas by several different routes. Those routes were seen as contriving to provide the basis for an attentional mechanism, in which the key components are certain parts of the thalamus, and related structures. Avoidance of pain is a primitive but important aspect of attention, and it is noteworthy that the intralaminar neurons in the centralis lateralis (CL) and parafascicularis (Pf) nuclei of the thalamus react specifically to pain, but only in the *awake* primate (Bushnell and Duncan, 1989).

That attention plays a vital role in the acquisition of new context-specific reflexes is demonstrated by an example of pain-provoked attention recounted by Claparède (1951). It concerns a female victim of Korsakow's syndrome, who was 47 years old at the time. As Claparède described it; 'the woman forgot from one minute to the next what she was told, or the events that took place. She did not know what year, month and day it was, though she was being told constantly. She did not know her age, but could figure it out if told the

date'. Similarly, she failed to recognize faces, even of those with whom she was in frequent contact. Claparède's narrative continues:

> I carried out the following curious experiment on her: to see whether she would better retain an intense impression involving affectivty, I stuck her hand with a pin hidden between my fingers. The light pain was as quickly forgotten as indifferent perceptions; a few minutes later she no longer remembered it. But when I again reached out for her hand, she pulled it back in reflex fashion, not knowing why.

The initial pain had clearly been instrumental in the acquisition of a new reflex associated with a specific context, namely the image of Claparède reaching out for her hand, and it served in the avoidance of pain even in the absence of recognition of its cause.

There are grounds for optimism that the controversy mentioned above — the one concerning the Cb at least — is well on the way to resolution. Tesche and Karhu (2000) have reported the results of a magnetoencephalographic investigation in which oscillatory responses in the ranges 6–12 and 25–35 Hz were detected in the Cb when there were random stimulus omissions during the intermittent electrical stimulation of a finger. They found indications that the neuronal reverberation provoked by the somatosensory stimulation lasted for 2–4 s. Moreover, the observed cerebellar activity was enhanced by attention. As Ivry (2000) noted, this work; 'provides strong evidence that the Cb in humans is activated in anticipation of somatosensory events, even when these events do not require overt responses'. This is just what the model described in this communication, and Fig. 8 in particular, suggests should be the case.

To sum up, then, it has here been suggested that the basic behavioral strategy of Earth's creatures has not changed in the four billion or so years since the evolutionary ascent started from the last universal ancestor. That strategy is one of self-paced probing of the environment, and cognition has been conjectured to be fundamentally related to the mechanism that makes the probing possible. Creatures can be said to know with their bodies, therefore, irrespective of whether they possess a nervous system. The advent of membrane excitability, and later of actual neurons, speeded up the transmission of information within the body, and one felicitous result was the emergence of the reflex. This permitted movements that were no longer provoked exclusively by conditions and events inside the creature's body.

The evolution of neural circuits increased the repertoire of movements, both by delegating responsibility for rhythmically repeated movements to sub-circuits (as typified by those found in the lamprey) and by permitting the selection of more complex sequences of move-

ments (an example being the premotor component in the honeybee). Generation of spatiotemporal patterns of neuronal signals (like those seen in the locust) was exploited in the interfacing of sensory input to sequenced motor output, and there is much evidence that this type of signaling is employed in the mammals.

The collective functioning of groups of components led to further improvements in performance, examples in the mammal including the BG and the Cb, and differentiation into a great variety of specific reflexes was particularly well served by the evolution of specialized sub-areas in the cerebrum. But the overall behavioral strategy remained the same, signals converging on the motor output areas as they have always done. Creatures continued to know with their bodies.

The most spectacular feature to evolve thus far has been that seen in the mammals, and it permitted acquisition, during a creature's own lifetime, of novel context-specific reflexes, especially those relying on sequences of muscular movements. This mechanism makes heavy demands on the neural circuitry, because it requires an attentional mechanism. And because attention must, perforce, be an active process, there had to be feedback from the muscles, carrying information about their current state, including their current rate of change of state. Without such information, anticipation would be impossible, and without anticipation there could be no meaningful adjudication and decision as to the most appropriate way of continuing an on-going movement. Without such a mechanism, novel context-specific reflexes could not be acquired.

The fascinating thing is that access to such on-line information mediates consciousness, the gist of which is the ability to know that one knows. This ability was clearly not there in the bacterium, and even creatures such as the honeybee lack it because they do not possess the required re-entrant circuitry required for context-specific attention. That the demands on the circuitry were indeed considerable is seen in the fact that such groups of components as the BG and the Cb had to develop heterogeneous structures, to permit what could be called the requisite multi-tasking.

The ability to know that one knows is referred to by psychologists as first-order embedding. Higher embeddings, such as that exemplified by knowing that one knows that one knows, merely depends upon the ability to hold things in separate patches of neuronal activity in working memory. This manifests itself in the creature's intelligence, which also dictates its ability to consolidate existing schemata into a new schema.

Finally, concerning the seemingly thorny problem of what is being reported to, consistency demands that this too is the body. So when we know that we know, the muscular apparatus is not only monitoring its own state, it is monitoring the monitoring. The present author is well aware of the fact that this may seem like

a tall story, but as this communication has noted, there is much to support it.

Thinking is a bodily function.

Acknowledgements

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