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SEVENTY-THIRD  
JAMES ARTHUR LECTURE ON  
THE EVOLUTION OF THE HUMAN BRAIN  
2003

EVOLUTION, COGNITION,  
CONSCIOUSNESS, INTELLIGENCE  
AND CREATIVITY

RODNEY COTTERILL

AMERICAN MUSEUM OF NATURAL HISTORY  
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JAMES ARTHUR LECTURES ON  
THE EVOLUTION OF THE HUMAN BRAIN

- Frederick Tilney, *The Brain in Relation to Behavior*; March 15, 1932
- C. Judson Herrick, *Brains as Instruments of Biological Values*; April 6, 1933
- D. M. S. Watson, *The Story of Fossil Brains from Fish to Man*; April 24, 1934
- C. U. Ariens Kappers, *Structural Principles in the Nervous System; The Development of the Forebrain in Animals and Prehistoric Human Races*; April 25, 1935
- Samuel T. Orton, *The Language Area of the Human Brain and Some of Its Disorders*; May 15, 1936
- R. W. Gerard, *Dynamic Neural Patterns*; April 15, 1937
- Franz Weidenreich, *The Phylogenetic Development of the Hominid Brain and Its Connection with the Transformation of the Skull*; May 5, 1938
- G. Kingsley Noble, *The Neural Basis of Social Behavior of Vertebrates*; May 11, 1939
- John F. Fulton, *A Functional Approach to the Evolution of the Primate Brain*; May 2, 1940
- Frank A. Beach, *Central Nervous Mechanisms Involved in the Reproductive Behavior of Vertebrates*; May 8, 1941
- George Pinkley, *A History of the Human Brain*; May 14, 1942
- James W. Papez, *Ancient Landmarks of the Human Brain and Their Origin*; May 27, 1943
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- S. R. Detwiler, *Structure-Function Correlations in the Developing Nervous System as Studied by Experimental Methods*; May 8, 1947
- Tilly Edinger, *The Evolution of the Brain*; May 20, 1948
- Donald O. Hebb, *Evolution of Thought and Emotion*; April 20, 1949
- Ward Campbell Halstead, *Brain and Intelligence*; April 26, 1950
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- Clinton N. Woolsey, *Sensory and Motor Systems of the Cerebral Cortex*; May 7, 1952
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- Horace W. Magoun, *Regulatory Functions of the Brain Stem*; May 5, 1954
- \*\*Fred A. Mettler, *Culture and the Structural Evolution of the Neural System*; April 21, 1955
- \*\*Pinckney J. Harman, *Paleoneurologic, Neoneurologic, and Ontogenetic Aspects of Brain Phylogeny*; April 26, 1956

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- \*David P. C. Lloyd, *The Discrete and the Diffuse in Nervous Action*; May 8, 1958
- \*\*Charles R. Noback, *The Heritage of the Human Brain*; May 6, 1959
- \*\*Ernst Scharrer, *Brain Function and the Evolution of Cerebral Vascularization*; May 26, 1960
- Paul I. Yakovlev, *Brain, Body and Behavior. Stereodynamic Organization of the Brain and of the Motility-Experience in Man Envisaged as a Biological Action System*; May 16, 1961
- H. K. Hartline, *Principles of Neural Interaction in the Retina*; May 29, 1962
- Harry Grundfest, *Specialization and Evolution of Bioelectric Activity*; May 28, 1963
- \*\*Roger W. Sperry, *Problems Outstanding in the Evolution of Brain Function*; June 3, 1964
- \*José M. R. Delgado, *Evolution of Physical Control of the Brain*; May 6, 1965
- Seymour S. Kety, *Adaptive Functions and the Biochemistry of the Brain*; May 19, 1966
- Dominick P. Purpura, *Ontogenesis of Neuronal Organizations in the Mammalian Brain*; May 25, 1967
- \*Kenneth D. Roeder, *Three Views of the Nervous System*; April 2, 1968
- †Phillip V. Tobias, *Some Aspects of the Fossil Evidence on the Evolution of the Hominid Brain*; April 2, 1969
- \*Karl H. Pribram, *What Makes Man Human*; April 23, 1970
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- Marcel Kinsbourne, *Development and Evolution of the Neural Basis of Language*; April 10, 1975
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- Paul H. Harvey, *Comparing Brains*; March 20, 1990
- Jeffrey T. Laitman, *Evolution of the Vocal Tract and the Origins of Speech*; May 7, 1991
- \*Dean Falk, *The Evolution of the Human Brain and Cognition in Hominids*; April 14, 1992
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- Niles Eldredge, *Mind Over Matter: The Evolving Place of Humans in Nature*; April 11, 1994
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- \*Matt Cartmill, *Do Horses Gallop in their Sleep? Consciousness, Evolution, and the Problem of Animal Minds*; April 30, 1996
- John Morrison, *The Human Cerebral Cortex: Exceptional Capabilities and Unique Vulnerability*; April 8, 1997
- \*Ian Tattersall, *The Origin of the Human Capacity*; March 24, 1998
- Terrence W. Deacon, *Primate Mechanisms Underlying Human Brain Evolution*; April 7, 1999.
- \*C. K. Brain, *Do We Owe Our Intelligence to a Predatory Past?* March 20, 2000
- Pasko Rakic, *Evolution of Neocortex: Lessons from Embryo-archaeology*; March 13, 2001
- Antonio Damasio, *Emotion and the Human Brain*; March 5, 2002
- Rodney Cotterill, *Evolution, Cognition, Consciousness, Intelligence and Creativity*; July 17, 2003

\*Published versions of these lectures can be obtained from Publications, Dept. of Anthropology, The American Museum of Natural History, Central Park West at 79th St., New York, N.Y. 10024.

\*\*Out of print.

†Published version: *The Brain in Hominid Evolution*, New York: Columbia University Press, 1971.



James Anthony

JAMES ARTHUR  
1842–1930

Born in Ireland and brought up in Glasgow, Scotland, James Arthur came to New York in 1871. Trained in mechanics and gear-cutting, he pursued a career in the manufacture and repair of machinery, during the course of which he founded a number of successful businesses and received patents on a variety of mechanical devices. His mechanical interests evolved early into a lifelong passion for horology, the science of measuring time, and he both made some remarkable clocks and assembled an important collection of old and rare timepieces.

Early in this century James Arthur became associated with the American Museum of Natural History, and began to expand his interest in time to evolutionary time, and his interest in mechanisms to that most precise and delicate mechanism of them all, the human brain. The ultimate expression of his fascination with evolution and the brain was James Arthur's bequest to the American Museum permitting the establishment of the James Arthur Lectures on the Evolution of the Human Brain. The first James Arthur Lecture was delivered on March 15, 1932, two years after Mr. Arthur's death, and the series has since continued annually, without interruption.



## EVOLUTION, COGNITION, CONSCIOUSNESS, INTELLIGENCE, AND CREATIVITY

It is a great honor to be invited to present the James Arthur Lecture for 2003, and to contribute to a series that has shed light on so many aspects of brain evolution, structure and function. I have read a number of the earlier lectures and have been impressed by their collective breadth. They have spanned a spectrum that stretches from the size and shape of the brain down to the interactions between the nerve cells of which the brain is composed. Many of the presentations have addressed one or other aspect of consciousness, and the related issue of intelligence. I shall follow their lead.

There has been a growing feeling in recent years that the mystery of consciousness might be amenable to a scientific solution. That would be a spectacular achievement, because consciousness ranks alongside the origin of the universe, the unification of the four fundamental forces and the nature of time, as one of the last great intellectual challenges. And it enjoys a special place even in that celebrated company, because it is the phenomenon most closely related to us. Indeed, one could say that consciousness *is* us. As René Descartes famously put it: *Cogito, ergo sum—I think, therefore I am*. And thinking is something we all value. During his own James Arthur Lecture, Matt Cartmill (1996) asked how much payment anyone in the audience would require for taking a drug known to permanently remove the capacity for thought, while leaving all other bodily functions intact. There were no volunteers.

The magnitude of the challenge facing those who would elucidate consciousness must not be underestimated. A full explanation of the phenomenon would require more than just an account of how it evolved and how it arises as a consequence of the brain's anatomy and physiology. One would also have to show what advantage it confers. And beyond that, there would be the particularly difficult job of scientifically characterising the sensations and emotions that seem to be the phenomenon's hallmark. David Chalmers (1996) was not exaggerating when he called those latter issues the *hard problem of consciousness*, and he warned that they might be fundamentally unsolvable.

Hard problems often require drastic solutions. It frequently takes a revolution in our way of looking at things to overcome the impasse. And this invariably means questioning assumptions long considered valid. A good example is the assumption that mind can be neatly separated from body. We now use the term *dualism* for this idea, and it still enjoys wide support, not the least among religious people. Descartes was one of its most ardent advocates. Dualism regards mind and soul as two aspects of the same thing, so when the soul survives death, there is still a mind to make survival worthwhile.

Another assumption about consciousness is even more widespread. It is tacitly invoked by most scientists working in this area, and it has been part of the unquestioned picture ever since the time of Aristotle. This is the *stimulus-response paradigm*, and it views consciousness as intervening between detection of sensory input and the resulting reaction (see fig. 1, left). This is commonly regarded as obviously reliable because it appears to harmonize with common sense. For example, when the reader scans these words—a visual stimulus—he or she can contemplate their meaning and respond accordingly—by reading on, or by discarding my text and doing something else. It seems logical to conclude that the conscious contemplation is quite distinct from the response, that is to say the possible reaction.

I suspect that acceptance of the stimulus-response paradigm stems from knowledge of simple reflexes. The doctor taps me with his little rubber hammer, just under the knee, and up jumps my lower leg. Similarly, using other sensory pathways, my head turns instinctively toward a sudden sound or flash of light. In such cases, the stimulus-response paradigm just *has* to be correct. But the question remains as to whether it can be validly extended to consciousness. My suspicion is that it cannot, and that this is where the need for draconian measures arises. But before I can persuade you on that point, we will have to delve deeper into stimuli and the reactions they might elicit. So let us start by taking a closer look at responses.

### *The Primacy of Movement*

Elephants are said never to forget, though one could ask what they actually have to remember. Relatively little compared with us,

one might suppose, for they certainly can't match the richness of our culture and technology. But evolution is only marginally interested in such issues; they are important only insofar as they affect an animal's ability to survive until the age of reproduction. So what *would* an elephant have to remember? If one has never thought about that question, the answer may come as a surprise. An elephant has to remember no less and no more than every other creature that 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 the environment and within their own bodies. On the output side, therefore, all that an animal can ever do is *move*.

Note that I use the term *on the output side*, rather than *response*, which might seem more appropriate. I chose the former because I wanted to include reactions to the conditions *within* an animal's body, as well as reactions to external stimuli. And just as importantly, I avoided making any reference to nervous systems, because I wanted to include animals not possessing such things.

Let us consider one such lowly organism, namely the single-celled *Escherichia coli* bacterium that does yeoman service in our digestive system. This creature is important to the argument because it does not respond rapidly to external stimuli; it has no reflexes. When a *coli* bacterium swims in water, it meets as much resistance as we would when swimming in molasses. But it has to swim, in order to reach its food. There is a second surprise, however, because the bacterium has no senses; it does not know where potential food is located. Why, then, *would* it swim? The short answer is that it evolved to do so, because that proved to be a useful survival strategy. Let's take a look at that strategy, drawing on the brilliant work of Howard Berg (1993) as we go.

The bacterium is pushed through the water by its flagellum, which resembles a ship's propeller. Anti-clockwise rotation of that device, looking in the forward direction, produces forward motion. Clockwise rotation does not lead to backward travel, as might be expected; it causes the creature to tumble and change direction. The bacterium's movement is dictated by the conditions within its body—by what in a more advanced creature would be called its *drive*. The flagellum's rotation, clockwise or anti-clockwise, is specified by the

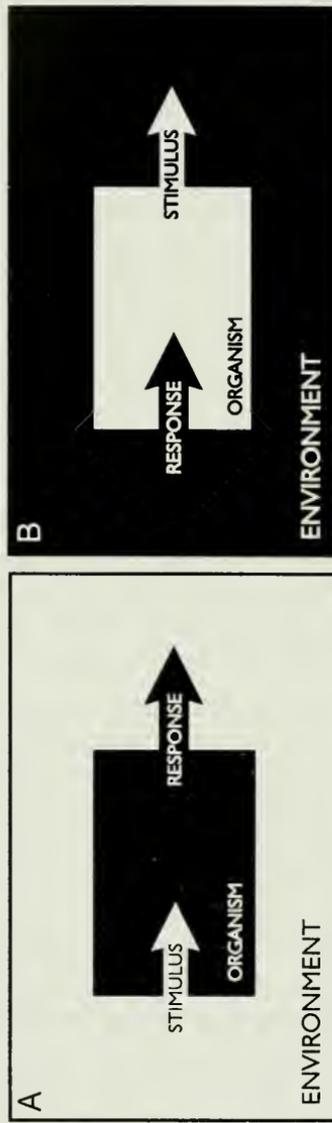


Fig. 1. The traditional stimulus-response paradigm (**left**) has been essentially unchallenged since the time of Aristotle. The author believes that this concept should be turned around (**right**) when considering consciousness.

concentrations in the creature's body of certain chemical compounds. Those concentrations, and thus the state of the drive, are determined by how much food the creature has collided with during recent seconds, and absorbed through its outer membrane.

If the internal chemical reactions detect that the food supply is adequate, the flagellum continues its anti-clockwise rotation and the creature continues its forward motion. If the food supply drops below the level required for survival, the bacterium tumbles and moves off in another direction. Such a diversion provides no guarantee that the bacterium will now be travelling toward plentiful food, but it's a better tactic than just doggedly staying on course.

In the case of the bacterium, therefore, the only stimulus is the one provided by its own motion, as it explores its surroundings, and the only response is the feedback from those surroundings, in the form of food the creature hits and ingests. This is just the opposite of a reflex. So the behavior of *E. coli* must be described in terms of self-paced probing of its surroundings (see fig. 1, right). And the current direction of rotation of its flagellum indicates what it has discovered recently about those surroundings, regarding the local distribution of potential food. Such acquisition of information can usefully be regarded as *cognition*, in a primitive form admittedly, but cognition nevertheless.

There will not be room here to discuss the behavior of many other species, but let us consider one at least, namely the honeybee *Apis mellifera ligustica*. As is well known, individuals of this species can gauge the direction and distance to a discovered source of nectar, and inform their hive-mates of this data, through their famous waggle dance. Karl von Frisch (1974) believed that their distance-measuring prowess stems from an ability to (unconsciously) record the amount of energy expended during the forage, but Mandyan Srinivasan, Shaowu Zhang, Monika Altwein and Jürgen Tautz (2000) have shown that the faculty has a different source. They made bees fly through a short tube whose inner surface was decorated with a pattern resembling a distorted chess board. Studying the subsequent waggle dance, the investigators noted that the bees were signaling a distance of several tens of meters, whereas a cache of nectar had been placed at the tube's other end, a mere meter away. The pattern's

black-and-white alternations had hoodwinked the insects' nervous systems into "believing" that they were registering the light-shade variations of their natural habitats, these usually occurring on a scale of several meters. This cunning study thereby established that a bee measures distance by recording the amount of "visual flow" (one form of sensory feedback) for a given amount of motion. This is clearly comparable with the mechanism we discussed earlier in connection with *E. coli*.

### *Cognition*

We can now return to my guess that science needs a sweepingly different approach in its ambition to solve the mystery of consciousness. *E. coli* and *A. mellifera ligustica* indicate that we need to turn things around. I am going to suggest that for the human being too, the relevant stimulus is the one associated with muscular movement, while the relevant response is the sensory feedback from the surroundings. I am thus proposing that our acts of cognition are always related to muscular movements, though these may be merely covert rather than overt—imagined rather than actually performed.

Let's take a closer look at these acts of cognition. They appear to be passive. We read the words on this page without seeming to move. But the eyes are actually moving a great deal of the time, as they scan the individual pieces of text. The importance of movement is familiar to the blind person, who is forced to read by moving the fingertips across the pattern of raised dots in a Braille text. A passive variant of such touch-mediated reading, with someone else moving the Braille text across the blind person's stationary finger, proves to be impossible. Switching to another sensory mode, we may assume that listening to someone speaking is a passive activity. Only when asked to repeat that person's words do we realize that we are silently mimicking what has been said. If we have not been paying attention, and thus covertly setting up the muscular movements required for articulation, we will not be able to recount what the other person has been saying..

This is such a central issue that it ought to be illustrated further. I am going to propose that we read three sentences *aloud*, even

though we might be alone as we do so. This talk was given at the American Museum of Natural History, so let's choose something from the animal world for the first sentence. Here it is: NO GNUS WERE FOUND IN THE BUSH, BUT SOME WERE SEEN ON THE VELDT. The second sentence is more generally familiar because most of us use word processors these days; it is: FINISHED FILES ARE THE RESULT OF MONTHS OF SCIENTIFIC STUDY, COMBINED WITH THE WISDOM OF YEARS. That is suggestive of hard work, so let's turn our thoughts to vacation for the third and final sentence. Here it is: THE FOREST RANGER DID NOT PERMIT US TO ENTER THE STATE PARK WITHOUT A PERMIT.

We are now going to make things more difficult, by carrying out a small task while reading those first two sentences a second time. We will count up the number of times we encounter a given letter, while again reading *aloud*, straight through and with no repeats. And we can give ourselves a good start by choosing the initial letter, N, for the first sentence. Here it is again: NO GNUS WERE FOUND IN THE BUSH, BUT SOME WERE SEEN ON THE VELDT. We make a mental or written record of the number of Ns we found, and then we proceed to the second sentence, now using the letter F as our target because that is now the initial letter. So here is that second sentence again: FINISHED FILES ARE THE RESULT OF MONTHS OF SCIENTIFIC STUDY, COMBINED WITH THE WISDOM OF YEARS. As before, we make a mental or written note of the number of target letters—Fs this time—that we counted.

Our second reading of the third and final sentence is less demanding; we simply read it aloud once more. Here it is: THE FOREST RANGER DID NOT PERMIT US TO ENTER THE STATE PARK WITHOUT A PERMIT. As Max Velmans (1991) pointed out, this sentence is interesting because it includes two occurrences of the six-letter sequence P-E-R-M-I-T, which we first pronounce *permit* and later pronounce *permit*. He suggested that this indicates that human information processing is not conscious—that it is, on the contrary, unconscious and automatic. I do not agree with that conclusion. If the six-letter sequence had appeared as the first word of the sentence, we could well have found it difficult to know how it should be pronounced. In other words, correct pronunciation requires detection of the relevant *context*. And such detection is not possible unless we have

adequate experience of reading English. But once we have mastered that (or any other) language, correct pronunciation can be achieved essentially as a reflex. Indeed, I am going to suggest that the evolutionary advantage of possessing consciousness is that it enables an individual to acquire and use novel context-specific reflexes within its own lifetime.

But what about those first two sentences, and our tallied Ns and Fs? What were our scores? I will guess that most people found all six Ns in the first sentence, or something close to that number. But how many Fs were there in the second sentence? The majority of people I've tried this test on managed to find only three, which was indeed my own score. It usually comes as a great surprise to discover that there are actually six Fs! How could we have overseen those three Fs in the three occurrences of the word OF? It is not because those words are small, because the same is true of the words NO, IN and ON, in the first sentence, and we did not miss the target letter Ns in them. The reason for our oversight is more subtle, and it is connected with the way the letters are pronounced. All six Ns in that first sentence are pronounced in the same manner. To use the term employed by the linguist, they all involve the same *phoneme*, and articulation of any phoneme involves activation of the appropriate muscles of the tongue, lips and jaw. But the Fs in the three occurrences of the word OF are pronounced as if they were Vs, and the phonemes for F and V are naturally different. This indicates that our nervous systems surreptitiously invoked the appropriate phoneme when we consciously attended to our letter-detecting task, and that our systems were thus duped by the duality of phonemes commonly associated with the written letter F.

This is a profound issue. It indicates that conscious attention to an observed stimulus, such as a written letter or word, has to activate the part of the brain involved in the appropriate muscular movements. It strongly suggests that conscious attention is an *active* process, never a passive one, as assumed in the stimulus-response paradigm. That latter view merely sees the muscle-directing regions of the brain as the *possible* recipients of the products of conscious processes occurring earlier in the system, closer to the sensory input.

But I am proposing that consciousness cannot be generated unless the brain's muscle-directing regions have actually been activated.

### *External and Internal Feedback Loops*

This has been a long but important digression. We can now return to the plot that was unfolding earlier. An animal can unconsciously pursue its four goals of feeding, fighting, fleeing and procreating. The conscious counterpart of such pursuit became possible only through possession of nervous systems having a certain type of internal feedback loop, one component of such a loop being the above-mentioned muscle-directing region. And consciousness is probably possessed only by mammals, though possibly also by birds. For all of them, movement—in either its overt or covert form—is the only means of accomplishing anything. This includes, as we have seen, the acquisition of information. Such movement produces sensory feedback from the surroundings, but the animal needs to be able to distinguish between self-provoked sensory feedback and sensory input that it has not itself caused, and which is thus not under its control—to distinguish between touching and being touched, for example. This requires that self-paced probing of the surroundings must be internally labelled, and the significance of its outcome evaluated. Such labelling and evaluation, together with the need for an attention mechanism, provide the basis of consciousness. They are, in fact, the source of our raw sensations. A study of the nervous system's circuit diagram (see fig. 2) components contribute to specific aspects of the overall consciousness mechanism, and we will be considering them in more detail below.

Meanwhile, the crux of the scenario I'm sketching is that our every movement puts a question to the surroundings. Every walking step we take asks *Is the ground still there?* Such questions are posed unconsciously, if we are sufficiently experienced at least, and the answer, *Yes, the ground is still there*, is just as unconsciously recorded. Only if something unexpected is encountered—a hole or a tree root perhaps—does the system detect the mismatch between the anticipated and actual outcome of its exploration. The abortive at-

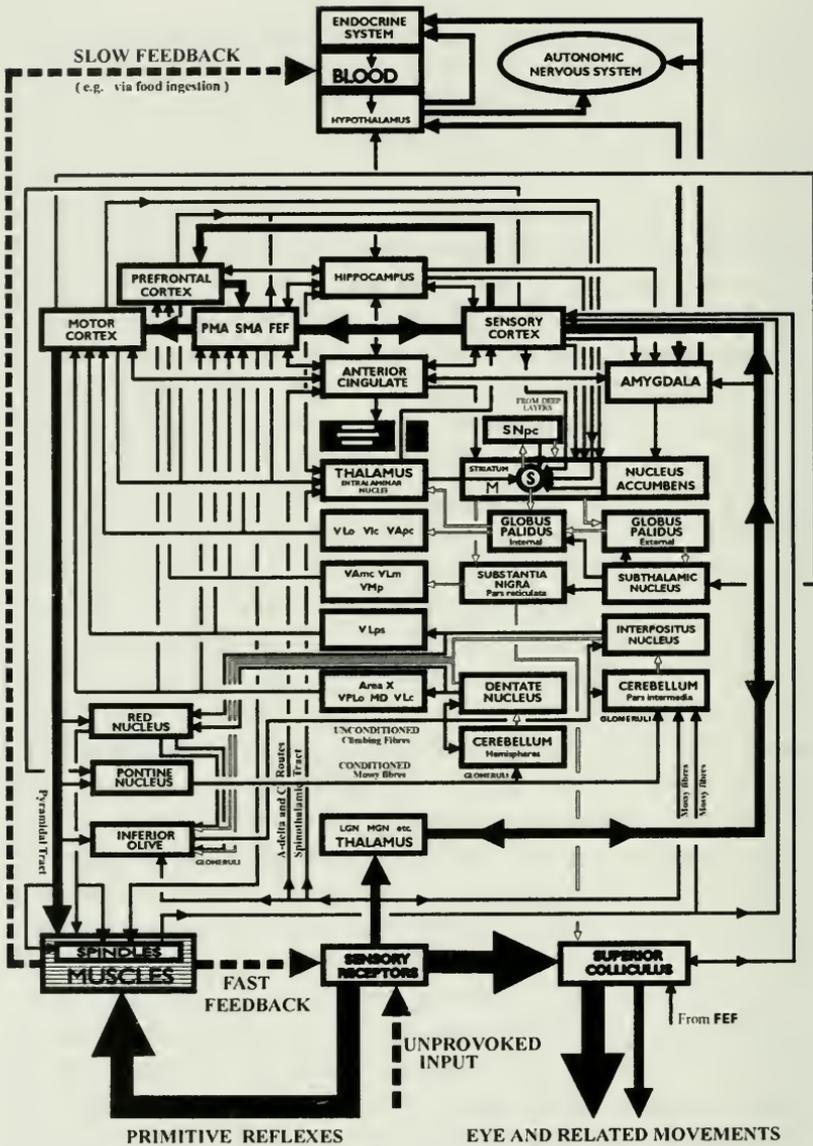


Fig. 2. An understanding of brain function requires knowledge of the nervous system's circuit diagram. As can be seen, this is reasonably complicated. But it can be rationalized in terms of the reversed stimulus-response paradigm advocated by the author (see fig. 1, right). PMA and SMA denote the premotor cortex and the supplementary motor cortex, respectively, and they collectively constitute the brain's motor-

tempt at movement then becomes the focus of attention, and of consciousness, if the creature possesses that faculty.

The requirement that the system is able to make predictions, and detect any mismatch, makes reasonably heavy demands of the underlying brain circuitry, not the least with respect to feedback loops. One could say that these are acting in parallel with the external loops that close through the surroundings—the ones that run from the animal's muscular movements, through the surroundings, and back into the system via the relevant sensory receptors. For example, my voice produces sound waves detectable by my ears. The internal loops can support the passage of nerve signals even in the absence of overt muscular movement, and when that happens, the animal merely thinks. Thinking is thus internal simulation of our muscle-mediated interactions with our surroundings. Whence our ability to imagine hearing ourselves speak.

We ought to pause at this point and consider attention in more detail. In creatures not possessing consciousness, priority amongst simultaneous sensory inputs is apportioned automatically, and it is hard-wired into the nervous system. So the sensory input exercising the strongest control on the reflexes, at any instant, is preordained. The plots of such creatures' lives could be said to be written in their genes. Their systems may be impressively sophisticated nevertheless. For example, a creature's movements will produce a great amount of sensory feedback that could be called routine, as when it touches its own body. It has to learn to ignore the nerve signals produced in that manner, and Christopher Miall, Donald Weir, Daniel Wolpert and John Stein (1993) have suggested that the cerebellum (indicated by DENTATE NUCLEUS, Hemispheres, INTERPOSITUS NUCLEUS, and Pars Intermedia in fig. 2) might mediate incorporation of these oft-repeated movement-and-feedback correlations into the creature's standard behavioral repertoire. Indeed, Richard Ivry

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planning region (FEF is the frontal eye field, which does the same job for the eyes). The author believes that the return routes (feedback loops) via which signals are fed from that region back to the sensory cortex are vital to consciousness. (A key to the other abbreviations is given in Cotterill, 2001b.)

(2000) has remarked that “there is strong evidence that the cerebellum in humans is activated in anticipation of somatosensory events, even when these events do not require overt responses.” And Masao Ito (1993) had noted several years earlier that the cerebellum exercises control over both overt movement and thought in essentially the same manner. Turning to the question of drive, creatures able to respond appropriately to a variety of different internal impulses must have a sufficiently differentiated control mechanism. In our own species and others close to us, this control is provided by the basal ganglia (indicated by SNpc, STRIATUM, NUCLEUS ACCUMBENS, GLOBUS PALIDUS Internal, GLOBUS PALIDUS External, SUBSTANTIA NIGRA Pars reticulata, and SUBTHALAMIC NUCLEUS in fig. 2).

But possession of these essentially autonomous mechanisms is not sufficient to produce consciousness. Sverre Sjölander (1997) has described the fragmentary nature of the typical snake’s behavioral mechanisms, and chronicled its ability to salvage a successful existence despite its various senses not functioning cooperatively. The inability of those senses to get their act together is known as the *binding problem*, and if that problem has not been overcome in a species, consciousness appears to be impossible (Cartmill, 1996). I have suggested (Cotterill, 1995; 1996; 1997) that the problem is absent from our systems, and from those of species close to us, because all nerve signals converge on the brain’s muscle-directing region (as distinct from the muscle-activating region, which in mammals is known as the primary motor area, indicated by MOTOR CORTEX in fig. 2). That region (which comprises the premotor area and the supplementary motor area—denoted by PMA and SMA, respectively, in fig. 2) functions as the source of the feedback signals—known as *efferece copy signals*—dispatched around the above-mentioned closed loop. Shigeo Kinomura, Jonas Larsson, Balázs Gulyás and Per Roland (1996) have used positron emission tomography to detect the activity in the loop’s various components during visual attention in humans. Another component in that loop is the nucleus reticularis thalami, which Charles Yingling and James Skinner (1977) have argued functions as a selective gate for signals passing from the thalamus to the cerebral cortex. And the nucleus reticularis thalami is itself under the control of the anterior cingulate

(see fig. 2) which is known to be the key recipient of nerve signals mediating the sensation of pain. We should not be surprised that a sentinel for pain plays a role in attention, because pain is always a possible outcome of the self-paced probing through which the system learns about the world. Returning to the muscle-directing region itself, as well as to Ivry's above-mentioned remark about anticipation, Jane Pedersen, Peter Johannsen, Christen Bak, Bent Kofoed, Knud Særmark and Albert Gjedde (1998) have shown that this part of the brain has to be activated when a human subject is expecting sensory input. This work added the important factor of cortical localisation to the earlier work of Hans Kornhuber and Lüder Deecke (1964), who monitored event related potentials from the scalps of subjects, and found significant features in their experimental traces about 800 milliseconds before actual movement. This "readiness potential" as they called it is a sort of advanced neuronal notice of impending action. One could use the term *bootstrapping* to describe the manner in which the components of the closed loop autonomously control attention, without dualistic intervention by any mystical external agency.

### *Consciousness and Emotion*

But why should things be arranged in just this fashion? How do the underlying anatomy and physiology conspire to produce the desired result? A somewhat indirect clue was provided by the work of Benjamin Libet, Elwood Wright Jr, Bertram Feinstein and Dennis Pearl (1979). They studied perception by patients awake during brain surgery (having obtained the patients' permission to do so, and exploiting the fact that the brain itself comprises no pain sensors). A brief tap on the back of one of the hands sends a signal to the appropriate part of the somatosensory cortex (part of the SENSORY CORTEX indicated in fig. 2) on the opposite side of the brain, the signal reaching that point after about 40 milliseconds. The awake patient naturally feels such a tap, and correctly locates it to the back of the hand. If the surface of the corresponding part of the exposed cortex is electrically stimulated, the patient again experiences a tingling on the back of the appropriate hand. However, Libet and his

colleagues discovered that such direct stimulation must be continued for at least 350 milliseconds for anything to be experienced at all.

The main discovery of the investigation was that conscious awareness of a tap does not develop until about 500 milliseconds—half a second!—has elapsed. This surprising result was arrived at by comparing the order in which the patient perceived two taps, a real one to the back of one hand and one elicited by direct stimulation of the cortical area corresponding to the other hand. (Details of the experimental protocol are rather complicated, and we shall not consider them here.) This half-second delay should be compared with the maximum time taken for signals to travel—using the nerve cells as “stepping stones”—across the entire length of the brain, via the shortest route, namely about 100 milliseconds.

Why should consciousness take such an extraordinarily long time to develop? What are the nerve signals doing during that half-second? The most obvious conclusion is that they are running around the brain's neural circuit (see fig. 2), and from what was stated earlier, it is apparent that a prime candidate for their route is the closed loop observed by Shigeo Kinomura and his colleagues (see above) to be activated by attention. Those signals would not be undertaking their circuitous journey just to consume time, however. They are modified as they travel, and one can imagine them provoking recall of past memories as they go. This seems to be a safe conclusion because the muscle-directing region is a major component on the closed-loop route, and as we noted earlier it is only through motor sequences—actually executed or merely imagined—that we can ever learn anything, that is to say acquire memories. Physicists use the term *self-organization* for such a process, and the system uses it in order to lock on to the sequence of muscular movements corresponding to a specific cognitive element.

A case in point was that third sentence we considered earlier, with its two different pronunciations of the six-letter string P-E-R-M-I-T. It can easily be shown that it takes a minimum of about 50 milliseconds to articulate a single phoneme, so even if we read the sentence as quickly as possible, we would not reach the first occurrence of that string of letters until after half a second had elapsed. During that period, our system would be articulating other unambiguous

words, invoking their meaning, and constructing the appropriate context. But we must bear in mind that this is possible only if we are sufficiently adept at using language. When learning to speak or read, we had to concentrate on every phoneme, and subsequently on every word.

A vital factor in our ability to manipulate and modify sequences of muscular movements—executed or merely imagined—is what Alan Baddeley and Graham Hitch (1974) referred to as *working memory*. The system has to be able to hold different possible courses of action in a temporary memory, while their relative merits are compared, and it must do so in relation to the prevailing external and internal conditions. One could loosely compare this mechanism with writing various alternatives on a blackboard, and then gradually eliminating the less-promising candidates, until a single possibility remained. Patricia Goldman-Rakic (1992) has made a strong case for such working memory being located in the prefrontal cortex, positioned at the very front of the brain. This region is known to have connections with many other brain regions, so it is ideally situated for the role of marshalling, organizing and coordinating the patterns of nerve signals that dictate the various muscle-directing scenarios. It is also significant that Joaquin Fuster (1985) has found that the persistence time of neural signals is longer in the prefrontal cortex than elsewhere.

One should not overlook the multiplicity of our behavioral modes; we underestimate the underlying complexity when we merely distinguish between consciousness and unconsciousness. The full inventory comprises the following: we can act without thinking, think without acting, act while thinking about that act, and act while thinking about something else. And although we might take it for granted, it is worth contemplating the fact that thought always has the greater priority; it is impossible to think about one thing, simultaneously do something else, and focus one's attention on the latter. Our thoughts are perforce always at center stage.

What aspects of the system's anatomy and physiology permit such a wealth of behavioral options? I suspect (Cotterill, 1998, 2001b) that a major role is played by the heterogeneity of structure found by Ann Graybiel and Clifton Ragsdale, Jr. (1978) in the striatum

(see fig. 2). They showed that this comprises two interwoven structures, both of which receive signals from the entire cerebral cortex, the overall effect being reminiscent of a patchwork quilt. The two components are now referred to as the matrix and the striosomes (denoted by the letters M and S in the box labelled STRIATUM in fig. 2). I believe that these two components are involved in overt and covert muscular acts (the latter mediating thought), and that they carry out their tasks individually when acts and thoughts run different courses. When we think about an act during its execution, however, the matrix and striosome components must function in unison. There is obvious scope for mutual influence between the two streams of signals, if they are related to acts that are rather similar. If I had recited Latin prose while the reader was tackling the "GNU" sentence above, my words would have had no effect, but if had switched to English, the reader might have had difficulty in concentrating on the task. And if I had also spoken of gnus, the reader might have become confused, and stopped altogether. Such interference was originally studied by J. Ridley Stroop (1935), and one can imagine it involving failure of mutual inhibition at the neuronal level.

Recalling that the basal ganglia (of which the striatum is a member) are intimately involved in the control of drive, one could loosely compare their role to that of an automobile clutch. And the parallel becomes a sad one when one notes that the underlying impairment in Parkinson's disease has been traced to a faulty substantia nigra (see SUBSTANTIA NIGRA Pars reticulata in fig. 2). The disease is characterised by jerkiness when the patient attempts to initiate movement, not unlike the jerky motion produced by the novice motorist's failure to smoothly employ the clutch. Lüder Deecke and his colleagues (1977) have reported that the "readiness potential" discussed above (Kornhuber and Deecke, 1964) is much diminished in Parkinson patients, and in some cases abolished altogether.

When the basal ganglia are functioning as they should, they are able to provide the drive that would, other factors permitting, lead to overt action; or to thought, or to a combination of both. There would then arise the question of how much harmony there is between the current drive and the current situation of the individual

within his or her surroundings, or indeed whether there is discord. I believe that this is the origin of emotion, harmony broadly leading to positive emotions and discord to their negative counterparts. It might even be valid to think in terms of emotional intensity being quantitatively determined by the degree of harmony/discord. The colloquial familiarity of the word *feelings* introduces a regrettable fuzziness here, because that term is indiscriminately applied both to emotions and to raw sensations. Modern neuroscience, on the other hand, sees the two concepts as being quite distinct, and it is for this reason that a separate term is usually employed in discussion of raw sensations, namely qualia (singular: quale). The quale associated with pain, for example, concerns itself with the actual *painfulness* of pain, rather than the mere fact of pain. I have suggested (Cotterill, 2001a, 2001b) that a quale of raw sensation is produced when a schema is accompanied by attention, a schema (plural: schemata) being 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. This sounds rather technical, I admit, but the crux of the matter is that schemata are the embodiment of the cognitive elements we considered earlier. We acquire such elements through experience, and it is important to note that they automatically imply an outcome of the relevant motor sequence. This is perhaps most directly illustrated by the bacterium we considered above, with its behavioral repertoire consisting of just two schemata; in the case of that creature we see choice telescoped down to a mere binary option. Seen in this light, emotion is an integral part of consciousness, so I would not agree with Jaak Panksepp's (2000) and Douglas Watt's (1999) separation of the two concepts (though I certainly admire their efforts at clinical explanations of the impairments of emotion).

I have introduced a number of technical terms, so we ought to pause and consider how they fit into the overall picture. Schemata are stored links between motor sequences and sensory feedback from the surroundings (which I've also been calling the environment). They are invoked automatically by creatures not capable of consciousness, and they can also be invoked unconsciously by crea-

tures possessing the capacity for consciousness. In the latter, schemata can also be invoked consciously, and incorporated into the creature's currently unfolding pattern of behavior. This ability requires considerable sophistication in the underlying neural circuitry. There have to be the internal feedback loops that mimic their external counterparts, the internal loops being able to invoke schemata off-line and compare them with what is transpiring externally. As discussed earlier, these loops emanate from the motor-directing region and are the conduits for efference-copy signals. The comparison function additionally requires an attention mechanism as well as a means of evaluation. When the creature merely thinks, in the absence of overt action, signals reverberate around the closed loops, and the existence of working memory permits comparison of—and choice between—competing schemata. In both the on-line and off-line situations, working memory also permits consolidation of existing schemata into novel composite schemata (Cotterill, 1994). And because evaluation must always be an integral part of this process, one could say that this is the origin of our capacity for reasoning.

Chris Frith (1992) has suggested that the alien voices heard by victims of schizophrenia are really the inner voices of their own imaginations, the erroneous perception stemming from a failure of the efference-copy mechanism. It seems likely that such failure is the result of malfunction at the biochemical level, rather than of anatomical pathology, because the condition appears to be ameliorated by appropriate medication. Moreover, the schizophrenic person nevertheless retains the capacity for consciousness, so the fault must be rather selective. Something superficially resembling an efference-copy mechanism was invoked by Germund Hesslow (1994), when he considered the nature of thought, even though he did not use that now-standard term. But he considered the internal loop as having arisen as a sort of embellishment of the reflex route, embodied in the stimulus-response paradigm that I criticised at the start of the present essay. Hesslow acknowledged the writings of Alexander Bain (1868) as one of the inspirations for his ideas, though Bain was a forerunner of the now-defunct behaviorist school. I feel that Hesslow put the cart before the horse, and that his view misses the

vital factor of (internal) drive and the primacy of the self-paced probing mechanism.

Let me enlarge upon that. The idea that thought is merely internal simulation of our interactions with our surroundings is rather obvious. One could even ask what else could it possibly be! But it would be fallacious to conclude, as Hesslow (1994) appears to do, that such simulations became possible when the system merely learned to internalize processes that had until then been purely external. That would permit the bizarre possibility that there had been pre-conscious speech, for example. The view I'm expressing here is diametrically opposite. It says that the novel-schemata-acquiring and novel-schemata-using faculties—including speech—which provide consciousness with its decisive advantage were *not possible* until evolution had produced just the right type of neural circuitry. The word *just* is important here. It seems highly unlikely that complexity of the type shown in figure 2 could have arisen without there having been simpler precursors. And there is much evidence that this was the case. The prediction-mediating cerebellum, for example, is seen in relatively primitive creatures which are unlikely to possess consciousness. And efference-copy feedback loops were invoked by Erich von Holst (1957) for the somewhat prosaic job of correcting for retinal slip when the eye and the head are moving simultaneously, this servo mechanism being envisaged to function unconsciously. I believe the vital evolutionary step was establishment of new connections between brain components that already existed, and which were already serving other less sophisticated tasks. (The high degree of cooperativity required between different brain components, if consciousness is to be possible, is emphasised in the views expressed by James Houk (1989) and more recently by Peter Gilbert (2001).) When those new links appeared, the brain acquired its present capacity for covertly running internal simulations of what it was simultaneously achieving through its overt and unconscious muscular activations. When that happened, consciousness had arrived on the scene!

### *Evolution, Novel Context-Specific Reflexes and Dreaming*

But what is the evolutionary advantage of consciousness? What role does it actually play? Why could a non-conscious but otherwise

human-looking creature not achieve the same things we do, in a totally automatic fashion? This is the so-called zombie argument, first raised by Robert Kirk (1974). The answer lies in that innocent-looking need to distinguish between external sensory input and sensory input the creature itself has provoked, when the prospect of novel behavior is in the offing. This is vital, because the creature can control only the latter variety of input. In default of its being able to make the distinction, the creature will not be aware that it is the agent of its own actions.

But why should having such a discriminatory mechanism produce consciousness? Why should the experience of raw sensations be the crucial factor? Ned Block (2002) tells a story—apparently ancient among philosophers—about a biographer who is researching for a book about Mark Twain, and he gradually becomes aware that there is a mysterious second person, named Samuel Clemens, who seems to have led a remarkably similar life, almost as if he were acting as Twain's shadow. Everywhere that Twain went, Clemens went, and everything that Twain did, Clemens did too. Finally, it dawns on the writer that Twain *was* Clemens, and that Mark Twain was merely a pseudonym. I believe that the same is true of what we have just been discussing. Those raw sensations, and the awareness they mediate—vitaly permitting the animal to distinguish between the different types of sensory input—imply *are* consciousness.

And this reveals the *raison d'être* of the phenomenon, because that ability to make reliable distinctions permits augmentation of the unconscious movement repertoire that the animal was born with. Consciousness enables an animal to acquire new context-specific reflexes—new schemata indeed—during its own lifetime. The reader is using such acquired reflexes as these words are read. They were certainly not there at birth. They had to be learned, and such learning involved the discrimination that is the hallmark of consciousness.

We ought to look at that learning mechanism in more detail, and let's return to those questions asked about the ground by our moving feet. They can be made unconsciously because we are expert at walking. But when we were learning to walk, each tentative step had to be the focus of attention. Similarly, when learning to speak, we carefully intoned each syllable, linking those sound fragments

together to form words. The same applied to our acquisition of reading. Once we had developed the necessary expertise with these things, however, we could walk, talk and read without having to concentrate on the individual steps, syllables and letters. Our focus of attention could then be directed toward the broader goals of many-step journeys and many-word sentences.

Ian Tattersall (1998) considered the evolution of the human capacity in his own James Arthur Lecture, and showed how this expanded as the front of the brain became larger. That part of the brain houses the prefrontal cortex, as was discussed earlier, and it seems logical to conclude that the gradual augmentation of our faculties was a result of an increased ability to manipulate schemata, and to consolidate them into increasingly sophisticated versions. Support for this view comes from the appalling injury sustained by Phineas Gage in 1848 (Harlow, 1868). He inadvertently created a spark while compressing a charge of gunpowder with an iron tamping rod, and the ensuing explosion drove the rod through the front of his head. The case is an important one in medical history because the damage brought about a dramatic change in Gage's personality. Originally polite, gifted and conscientious, his post-trauma state was characterised by shiftlessness and frequent lapses into profanity. The recent computer-aided reconstruction of an image of his brain, using his surviving skull, by Hanna Damasio and her colleagues (1994), demonstrated that Gage's prefrontal cortex had suffered massive damage, whereas his motor-directing areas had been spared. This conforms with the ideas I have been expressing, because such injury would have severely curtailed his higher faculties, while not precluding consciousness.

We have not yet considered the actual mechanism whereby novel schemata are incorporated into the creature's behavioral repertoire. As a preliminary, let us consider the central role played by the muscle-directing region. It must orchestrate the movements of all the skeletal muscles, making sure that conflict does not arise (Cotterill, 1995). Let us consider a simple example. A specific pattern of muscular movements will raise my hand to my mouth and place some of my fingers between my teeth. Then another set of muscular movements will cause my teeth to bite through my fingers and sever

them from my hand, with attendant pain! This doesn't happen of course, because my trained system knows all about the danger. So even when my attention is otherwise directed toward a conversation while I am eating, my system automatically prevents me from invoking and activating a finger-biting schema. I'm sure that I did bite my finger a few times during infancy, however. I suspect that the system incorporates knowledge of such adverse experiences (and of course their positive counterparts) into its repertoire during dreaming, and it is interesting to note that infants spend much more time than adults in the dreaming state. In his James Arthur Lecture, Matt Cartmill (1996) opted for the ingenious theory of dreaming put forward by Francis Crick and Graeme Mitchison (1983), which postulates that it serves to eliminate accidentally formed—and unwanted—memories. I find it difficult to believe that a system prone to such erroneous storage would have survived in the evolutionary arena.

My view appears to harmonize with results reported by Robert Stickgold (1998), who found evidence for consolidation and integration of memories during sleep, including its dreaming phase, and highlighted the interaction of the hippocampus (see fig. 2) with the rest of the cerebral cortex. Brenda Milner (1967) had demonstrated the major role played by the hippocampus in the laying down of long-term memory, through her observations of the patient H.M. following bilateral removal of his hippocampus. These observations were subsequently reinforced and extended through Larry Squire's (1992) studies of members of several different mammalian species, all of which had had the hippocampus removed. It is now widely believed that the hippocampus serves as a temporary depository for short-term memories that are candidates for longer-term memory storage, the actual storage being elsewhere—and widely distributed—in the cerebral cortex. Alexei Egorov, Bassam Hamam, Erik Fransén, Michael Hasselmo and Angel Alonso (2002) have recently discovered how this might be coded for, because they have found hippocampal neurons whose activity level depends in a stepwise manner on how much input they have received during the previous few seconds.

Dreaming sleep is now more commonly referred to as rapid-eye-

movement (REM) sleep, because the eyes have been discovered to move about erratically during this phase. It was previously believed that the eyes were serving a dreaming counterpart of wakeful vision during such episodes. But perhaps the real explanation is more down-to-earth. The point is that all the other skeletal muscles are immobilized during REM sleep, presumably because the schemata-consolidation mechanism referred to above might otherwise cause the limbs to move (something which does in fact occur in certain pathological conditions). But with the eyelids closed, the eyeballs would be free to move without causing any sensory input. But there is more to this story, because the muscle-immobilized REM period is limited to a few minutes, in order to ensure adequate blood circulation (the recent cases of deep vein thrombosis during long air journeys serving to illustrate that point). But the corneas of the eyes also contain blood vessels, and the rapid movements of the eyes against their lids might be nothing more sophisticated than a periodic bout of massage!

Returning to the idea of schemata consolidation during dreaming, this concept recently received endorsement by Robert Stickgold's group (Mednick et al., 2002), who demonstrated that short bouts of sleep can prevent perceptual deterioration. Commenting on this fascinating finding, Pierre Maquet, Philippe Peigneux, Steven Laureys and Carlyle Smith (2002) wryly noted that it is a good idea to occasionally be caught napping! Amir Mazur, Edward Pace-Schott and J. Allan Hobson (2002) have recently made observations which suggest that the differences between the self-awareness typical of waking and its diminution during dreaming may be due to biochemical deactivation of the prefrontal cortex in REM sleep.

### *Intelligence and Creativity*

One attractive consequence of the theory of consciousness I have been sketching is that it leads to what I feel is a believable account of intelligence. It views this as simply the ability to link together elementary muscular movements—actual or merely simulated during thought—into more complex movement patterns. If that is a reliable picture of intelligence, it would suggest that children who

experience difficulties with spoken language—which involves the muscles associated with the voice of course—might also find it hard to execute flowing movements with other muscles. It was thus an exciting scientific development when Philip Teitelbaum and his colleagues (1998) found that autistic children display precisely such difficulties.

Not all autistic children have diminished intelligence, admittedly, though the great majority of them do have lower-than-normal IQs (Frith, 1989). The infirmity cannot be diagnosed reliably until the end of the second year, because the pediatrician would like to check whether there are difficulties with language. But studies of videos taken of children at the age of three months, well before they were diagnosed with autism, have revealed that there are indeed early signs of difficulties with the linking together of elementary movements. If a normal child is lying on its back, and wants to roll over onto its stomach, it soon learns that a twist of the head, followed by a twist of the shoulders, and then by a twist of the hips, leads to a rolling motion requiring a minimum of effort. But yet-to-be-diagnosed autistic infants experience great difficulty in performing such sequences, just as they will later encounter trouble in joining words together to make sentences.

Another consequence of these ideas is that it makes sense to talk of intelligence only in the conscious animal. An animal not possessing consciousness may be capable of impressively intricate patterns of movement, but these are executed automatically, and the repertoire is never expanded during an individual's lifetime. Let us briefly return to honeybees, and note that despite their abilities to gauge direction and distance they are not able to additionally signal flower type to their hive-mates. Given sufficient time, however, bees with that ability might evolve. But their thus-augmented signalling capacity would not indicate acquisition of consciousness; they would still be functioning as unthinking automatons. Martin Hammer's (1997) circuit diagram of the honeybee's nervous system shows why this is the case. There are in fact internal feedback loops, which mediate associative reward learning, but there is nothing that even remotely resembles the attention mechanism shown for the mammal in figure 2.

Finally, the theory presented here suggests that creativity must be related to the ability to explore novel linkages of elementary movements. This might sound like an impoverished view of that faculty. It might seem to be applicable to sports people and ballet dancers, but what about creativity in the other arts and in the sciences? The answer lies in the fact, so easy to forget, that our only output is movement, and that all mental processes ultimately must be related to those activities in the brain that dictate the contraction of our muscles. The logical conclusion is that candidate novel schemata must vie with each other, while being checked for fulfilment of the constraints mentioned earlier. And it is natural to assume that the muscle-directing region must be intimately involved in this fitting process. This will probably manifest itself in individual neuronal activities racing each other toward a threshold level, as envisaged by Roger Carpenter (1999). But there must be other factors at play, because a race will produce only familiar winners in the absence of new runners. What is the origin of the latter? Perhaps it lies in the ability of the circuit to capture novel correlations between neural signals, by dint of the feedback routes known to exist within the cerebral cortex (Felleman and Van Essen, 1991), as opposed to the feedback loops involving subcortical components, as discussed above. Claus Nielsen and I briefly discussed the possibility of “reverse-projection learning” (Cotterill and Nielsen, 1991), and the situation was subjected to a more thorough analysis by Wolf Singer (1995). It might be particularly significant, in this respect, that Semir Zeki and Stewart Shipp (1988) found a greater spread among the cortical reverse projections than they did among the forward projections. This is suggestive of the system unwittingly capturing unsuspected correlations between its input signals, and subsequently being able to act upon what the system has discovered. Perhaps this is why we are often oblivious of the origin of our bright ideas. And given what was stated earlier regarding schemata consolidation during sleep, this might explain why it is that we sometimes wake with the solution of a problem that we went to bed with.

Before closing, and because I have been speaking in a museum that concerns itself with many different species, I feel that I ought to make a guess as to which of these possess consciousness. Mindful

of that principle of self-paced probing of the surroundings, I am going to suggest that the existence of *play* among the members of a species is possibly the best indication we could have that consciousness is present. Why otherwise would the young of a species “waste” their time cavorting and gamboling about. A zombie wouldn’t be caught dead indulging in such seemingly useless activity! But it’s just the sort of thing that individuals would do if they are able to learn new tricks by periodically challenging their environments to produce novel feedback. I do not have exhaustive data on this point, but it seems to me that all mammals play, and my guess is that they all possess consciousness. This means, *inter alia*, that they must all be able to experience pain. It behoves us to be kind and caring toward them.

In sum, then, there seem to be ample rewards for taking the diametrically opposite view to the one embodied in the venerable stimulus-response paradigm. It is a surprising story, but I believe that Aristotle and Descartes would have found it intriguing.

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