How It Is to Be the Brain of a Monkey*

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Monkey, Cortex, Social, Time, Perception

Hypotheses are presented on neural peculiarities of the monkey brain that distinguish monkeys from other mammals and man:

- The unique feature of cortical tissue is that it can be applied serially. It fulfils some requirements of a powerful visual system.
- The richness of visual as compared to other signals has yielded a basis for recognizing the bodily similarity of oneself to conspecifics. A visuo/motor coupling trained on oneself but applied to conspecifics ("aping") evolved.
- Long series of (generalized visuo/visual) computations feasible in a very large cortex would produce excessive delays that would not correspond to outer world delays. The new human solution to this is an "offline" system in which temporal relationships are described by excitation patterns. This gives rise to a rapid expansion of the cortex.
- In humans, a "meaning" has to be attributed to the mutual (computational) relationships of excitation patterns in the offline system, by a reference to the corresponding relationships that would be valid in the normal (online) system. "Perception" is a corollary of this.
- The offline treatment of time, together with "aping", leads to new types of helping and other social interactions.
- Monkeys may be compared to humans not using their offline system in the state of "absent-mindedness".
- Experimental approaches departing from excitation patterns are discussed.

The purpose of the conference "Natural Organisms, Artificial Organisms, and Their Brains" was not to present results, or overviews, but to discuss open questions. The present contribution is in this spirit.

I am concerned with four problems:

(a) Brains of monkeys are studied because of their similarity to those of humans. It is my impression that the differences to humans are not well delineated: monkeys are often implicitly assumed to be animals that lack human-like language but otherwise have the same but *quantitatively* less evolved faculties as humans. If it is stated that a task is too difficult for a monkey the reasons for this are not clear.

(b) Progress in behavioural research frequently reveals that animals other than mammals, some of them having small brains, can show performances that previously had been thought to require a highly evolved mammalian brain (see e.g. Giurfa and Menzel, 1997). The urgent question is then why the brains of mammals, in particular of those of primates, are so large.

(c) Neurophysiological studies in mammals tend to reveal functions which one would expect in brains of widely varying types and sizes, such as sensorimotor integration, selectivity for stimulus features (that may or may not depend on reward training), or traces of memory.

(d) The large mass of cortical tissue in primates contrasts with a lack of general specification of its role. So far no function is known, except for human language, that can only be achieved by cortical tissue.

A collection of hypotheses on the neural nature of the monkey is presented here that is composed of six parts, concerning (1) vision, (2) "aping" (which is the faculty to copy an action of a conspecific without understanding its goal), (3) a general

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role of the cortex, (4) the processing of time, (5) differences to humans, and, as a conclusion, (6) the nature of the monkey. A section on experimental questions is appended.

Some of the hypotheses may not appear well-founded, partly because they also contain statements on what will *not* be found. Such statements are notoriously difficult to prove experimentally. Also, one should bear in mind that this is not an overview, nor is it a theory, but a proposal for discussion.

(1) Vision

An optically well-designed eye presents so much valuable information on many parallel channels to an organism that even a highly sophisticated brain cannot fully make use of it.

Often it is asserted that an animal not using available information does not need it. This is equivalent to predicting that the species to which the animal belongs will not evolve towards a better use of that information.

Large amounts of possibly relevant signals, containing numerous internal correlations, and relationships to own movements, are available even from large distances. An immense world, largely absent for the other senses because either only events changing in time are signaled, or only short distances are covered, becomes accessible through the sense of vision.

Evolution has advanced primate vision beyond optokinetic and flow field analysis, and beyond vision by "type of object" (see below), making use of precise transformations of visual signals when a far object is inspected from a close distance, when it is translated, rotated, deformed, illuminated, or partially hidden. The primate visual system provides efficient means of classification and generalization of object features and relationships to own behaviour, facilitating compact storage, and enabling the animals to handle large amounts of associations, first of all the completion of invisible back sides of objects. The latter procedure may comprise the establishment of an abstraction, or "compound view" from several views of which some are incomplete (learning stage), and thereafter to deduce the entire compound view from one incomplete view (application stage).

The stress of the description is on the efficient *handling* of the visual signals, but not on the system being able to react to features, nor on low-level properties such as visual acuity. To illustrate the issue, humans can easily see every detail of a random dot pattern, but they cannot handle hundreds of such patterns if their difference is only in the generating set of random numbers. For this type of picture, classifications, generalizations, associations, storage or retrieval cannot be organized efficiently by the human visual system. Similarly, a bird can see the details of finger positions and skin wrinkles on the hand of a monkey but certainly it cannot organize the handling of hundreds of such views.

Note that in the description the term "perception" does not occur. Perception is a process known to humans only introspectively, and it is experienced as if it was a process that has input signals but that may have no output at all. The hypothesis is that a monkey is perfectly able to see, to handle visual signals from a great variety of sources, to produce memory traces and to derive behaviour, but that no perception occurs. Point (5) will elaborate on this topic in more detail.

(2) "Aping"

This is the ability of visually copying the behaviour of conspecifics or even man. Its cerebral prerequisites are substantial.

In a first step, high-level object vision has to be applied to visible parts of the monkey's own body, say, its hand. The total amount of neuronal information from one's own hand may to a large extent be visual if very accurate transformation rules and numerous generalizations on hand deformations, finger positions and skin wrinkles are available from vision. Additional informations (tactile, inner tension signals, reactions to motor commands) may then become a minority so that finally the *majority* of signals from one's own hand (namely the visual ones) become similar to those obtainable from a hand of a conspecific. With the appearance of monkeys, the nervous system can begin to make use of the idea that the own hand is in a certain sense comparable to that of a conspecific. The hypothesis is that the excellent ability to complete partially visible objects finally enables a monkey to make use of the fact that it is bodily similar to its conspecifics.

This ability must not be confused with the obvious ability of *all* animals to recognize its conspecifics. This does not require to make use of the similarity of oneself to one's conspecifics.

Another prerequisite of "aping" is to be able to establish a "backwards" link between the visual consequences of an action done by oneself, and the motor commands used for that purpose. Normally one first generates motor commands, and then one may observe the results on one's own body. Now the visible results are required as primary events. Therefore they must be associated with some delayed motor commands so that later, upon appropriate visual input, the associated motor commands can be retrieved. Possibly sensory feedback from motor output (joint receptors, muscle spindles) play a role. This system is similar to the parrot's audition-and-voice association device. The outcome is a visual representation of one's own motor commands. The hypothesis is that monkeys have such a representation. There are some neurophysiological hints to this (Hyvärinen, 1982; Di Pellegrino *et al.,* 1992; Rizzolatti and Arbib, 1998).

The sequence of steps in an actual act of aping are as follows. In the case of "aping" of the opening of a water tap, the first step is the observation of a conspecific or a human turning the handle, and the water jet appearing. Since "aping" usually is not intended to occur synchronously with the original act done by someone else, the animal immediately has to associate the tap with the visually observed acting individual, by an appropriate alteration of transmission efficiencies of Hebbian synapses.

In such a situation there are no repeated events, but the animal knows during or shortly after the event that it was relevant. The hypothesis (not limited to monkeys) is that very generally, upon a fulfilment of a Hebbian condition, synaptic strengths are altered rather strongly so that a single such event would be sufficient for durable storage. However, if nothing else happens, the strong alterations would fade to a weak value which would need several repetitions to be strong enough for a memory trace to be retrievable. In contrast to this, in a case as above the knowledge of the relevance of an event would be used to trigger a mechanism of arresting that decay, so that a single event can be stored permanantly. The rather unspecific control signal ("the observed event was relevant") is available within some 100 ms, and may often be prepared even before an action. This could be a role of widespread brain stem afferents to the cortex (see M. Koch, 1998: this issue, pp. 593–598).

Later, when the animal proceeds to the copying action it will only see the water tap. The hypothesis is that its visual association memory has first to complete the visually observed action of the now absent conspecific (in a similar way as completing a back side of an object), and thereupon that visually represented motor act has to be translated into real motor signals, by the newly developed visuomotor association system.

"Aping" in monkeys is not judged to be impressive by many observers. This seems partly due to an underestimation of the difficulties inherent in this process, and also due to the rapidity of monkey movements (for the brevity of the actions see also below). After a human has used a tool, and then leaves it behind, a monkey having access to the site would take it, handle it for less than a second, and then abandon it.

The hypothesis is that this type of activity, although rarely impressive, can already provide the animal with a bias to segregate important actions and objects from chance observations. The advantage is that the animal needs neither understand the purpose of the action, nor learn itself by repeated experience. When the animal, by virtue of "aping", is able to recreate the same circumstances (with itself as the acting individual) as the ones observed with another individual, then the chance is highly increased that it will grasp the usefulness of the action. What is needed, however, is to have some judgment of whether the actions of a particular conspecific or human are generally worth to be retained. Possibly this is a role of monkey rank order.

(3) Cortex

All animals have constructed neuronal networks for individual purposes, and construction procedures have evolved which can multiply the elementary processing unit in lateral directions: there are numerous examples of layered structures, such as the retina, which locally perform the same parallel signal processing.

However, most animals did not solve the corresponding serial problem: The signals leaving the retina cannot reasonably be processed again by another retinal network.

The hypothesis (not limited to primates) is that the cortex is an elementary neuronal network, composed of modules, or columns, whose essential advantage is that it can be applied *serially*. It can also be applied in parallel but this property is not new.

In this sense the cortical module is the re-invention of the neuron on the network level. In a convergent way the neuron can receive signals from many other neurons and, in a divergent way, it can send them to many further neurons which in principle can be built according to identical construction principles. There may be sub-varieties of neuron types which, however, still are considered as neurons. The connectivity between neurons can be altered by Hebb-like processes. There may be connection rules such as that certain inhibitory synaptic inputs terminate on the soma. The performance of a single neuron (as compared to a brain) is not very sophisticated. It may be described as a correlation detector or an integrate-and-fire device.

The last paragraph can be translated in a rather stereotyped way to apply to a cortical module instead of a neuron:

The cortical module can in a convergent way receive signals from many other cortical modules and, in a divergent way, send them to many modules which in principle can be built according to identical construction principles (see also Puccetti and Dykes, 1978; Roe *et al.,* 1992; Sur, 1993). There may be subvarieties of module types, giving rise to different cortical areas, which, however, are all considered as cortex. The connectivity between modules can be altered by Hebb-like processes (there is, at present, no evidence of whether some "compound Hebb process" exists that operates on the level of entire modules). There may be connection rules such as that certain layers preferentially connect to certain neuronal structures (e. g., layer 5 connects to the brain stem and spinal cord). The performance of a single module (as compared to a brain) is not very sophisticated. It is a task of brain research to find a general description for this. It would not have to be in terms of sensory input or motor output but it would rather have to link the direct inputs of a module to its outputs.

A tentative description (not a part of the hypotheses), giving an idea of how it might look like, is as follows: Assume that the number of cortical areas plus subcortical nuclei is N (between 20 and 1000). In ontogeny, select randomly some small fraction of these (say, the square root of N) as input sources. Take fibre bundles from the selected areae and nuclei, and send them into a module of one particular cortical area. Later in life, when significant neuronal activity is available, that latter module would search for correlations between all the inputs, strenghten the corresponding endings, and possibly even add modules where there is much correlation. Still later in life, in an "application" stage, this piece of cortex is then able to classify incoming excitations by the nature and degree of correlation. Using the picture of neuronal assemblies, the latter step would correspond to the ignition of an assembly. The output, depending among other things on the selection of fibre sources, is a classification result, and as such its overall information content is reduced, as compared to the incoming signals. The fibres carrying this output are then treated again as being one out of the above N types, and so on. Correlation and classification steps are concatenated, but by virtue of convergence and divergence, each time the signals from other sources are involved. Expressed in another way, the cortex is a machinery that can iteratively determine which excitations belong to one Hebbian neural assembly.

The hypothesis is that the evolutionary advantage of the cortex, in contrast to individually engineered networks, is that an ever-increasing amount of cortical tissue can be built without subjecting this increase to Darwinian selection with respect to processing performance. Thus, if there are solutions to secondary restrictions such as nutrition and space, then the cortex yields an advantage in *evolutionary speed*, and thereby flexibility, but not necessarily in absolute performance. Animals using individually tailored networks may solve the same problems much more elegantly, and with much smaller brains, but for this they would need much longer time in evolution (and thereby they possibly do not come into existence).

Thus, I do not believe that the human cortical language areae are specifically designed for processing language, but rather, that the use of general-purpose cortex, and of general routing rules, was the fastest way of meeting the then relevant evolutionary requirements. The reason for the inability of monkeys to speak is not that they lack a language "centre" or area. Rather, a number of processing prerequisites (based on a visual system with greatly extended purposes; see below) are required before on top of all this a language processing system can be installed. A great problem is to achieve a sufficient degree of data compression by providing for still more generalization and classification steps. I believe that the selection of the output channel (gestures, voice) is a minor problem (see also Rizzolatti and Arbib, 1998). However, to discuss this goes beyond the scope of the present contribution.

Stating that "a task is too difficult for a monkey" is analogous to stating that a monkey cannot speak: it does not mean that the monkey lacks a "centre" for that task. Rather, the number of concatenation, convergence and divergence steps, and the intricacy of how the necessary connections have been shaped during the animal's life, are insufficient, so that classifications and generalisations cannot be pushed to the levels where higher common aspects emerge that are required for the solution of difficult problems. One of the limitations is related to the processing of time treated below.

In some sense the cortex (and earlier in evolution, the neuron) is like money; it is always useful, before one knows precisely for what purpose it shall be spent.

(4) Processing of Time

The brain of every animal can cope with sensory and motor events that have to have an orderly temporal progression (see e.g. Gibbon *et al.*, 1997). The concatenation of brain events is "implicitly understood by the system" as that the events in the outer world happen at about the instant of occurrence of the accompanying excitation distributions. In other words, an animal "always lives in the presence". This does not mean that there is no dependeny on the past: memory of past experience optimally guides future bahaviour. It strongly influences which behaviour will follow a given *present* sensory influence. However, an animal cannot reanimate a single past event into a neuronal excitation pattern in order to derive new behavioural consequences from it. For this, a new actual experience has to be made.

This is "online processing". One would describe it by saying *how* to do something. To know how to drink a coffee means that Hebbian synapses are set in such a way that the entire procedure (including some bifurcations, to cope with variants) can be run with a minimum of "try and error". The synapse settings contain the ways to recognize a cup from the incoming sensory stream, and how to transform the stream stepwise to form adequate motor commands. However, there is no other way to run through such a sequence than by actually "doing it". The sequence stops if no cup is present. Also, there is no way to extract from the the synapse settings what a "cup as such" is, i.e. other uses than drinking a coffee (e.g. return it upside down and use it as a candleholder) cannot be derived; for this, the cup has to be inspected anew.

An online-processing system as described, while it can derive future behaviour in an optimal way from a present situation, cannot generate prediction in the proper sense which would be an excitation distribution describing some future situation *irrespective* of one's own behavioural reactions. For a further consideration of prediction see below.

To avoid frequently encountered misunderstandings, it is reiterated here that an online system is perfectly able to analyse temporally structured events and to generate temporally structured behaviour: if after some sensory input a very complex, time consuming computation is required, the ensuing behaviour will be correspondingly delayed. Online processing means that the event in the outer world giving rise to a sensation is assumed to take place about at the instant of the sensory excitations that are elicited. Similarly, the consequences of an action in the outer world are assumed to take place at about the instant of the motor excitations, no matter how large a delay might have been between the sensory and the motor events.

The hypothesis is that monkeys were the first to encounter cases where difficulties arose with this system: if a visual input triggers a lengthy computation whose purpose is to complete some associated but invisible parts of the scene then the problem is that there is one initial "direct" excitation distribution, and much later another, calculated excitation pattern, but *both refer to the same time in the outer world*. It is obvious that such a problem of time reference must arise when from a sensory input an excitation is computed which is equivalent to another *sensory* input. In contrast, even long lasting computations transforming sensory signals into motor activity proceed without conflicts. In fact, one day's life is a continuous chain of neuronal computations in which the contacts of the cerebral excitation distributions to the outer world via the sensory and motor interfaces wax and wane.

The main hypothesis of the present contribution is that monkeys have no solution to the above problem of time reference arising with sensory-sensory completion computations. Rather, like other animals, they have to limit the time spent for this type of computation to a time window that still allows to interpret direct and computed sensory excitations as occurring simultaneously. I believe that the width of this window is of the order of 100 ms at best. The total durations of the excitations involved may be longer than that, but when they are shifted in time against each other by more than the simultaneity window, a synchrony interpretation would no longer be possible.

If an acceleration can be achieved by breaking down the computations into several faster parallel processing branches (in different visual areas) then the problem can somewhat be alleviated. However, not every complex computing problem can be treated in this way.

Neurophysiological evidence for working memory may consist of a continuing neuronal excitation after a stimulus has been extinguished, enabling a trained animal to react with a delay of some seconds to a parameter (e.g., the locus) of the now invisible stimulus (Goldman-Rakic, 1987; 1996; Fuster, 1998: this issue, pp. 670–676). It might be argued that this is a counter-evidence to the above hypothesis, because it seems to indicate that the observed excitation refers to a past event in the outer world. This is certainly correct, but it is unlikely that the time of occurrence of the corresponding outer-world event is coded by that excitation pattern. At best it tells the rest of the brain that somehow there is no correspondence to a real, presently occurring outer-world event.

Obviously the task of completing a missing part of a visual scene becomes still more difficult if that part contains a relevant time structure. The hypothesis is that for this reason monkeys have evolved the faculty (also present in human imagery) to represent an observed action of a conspecific by a kind of motionless caricature, i.e. by replacing movement by typical positions. This can only work if the object (in general the conspecific) is sufficiently well known. Of course only short actions can be represented in this way, and the hypothesis is that this is the reason why monkeys can only achieve the necessary completion calculations of rather brief aping actions.

It is important to realize that the completion of visual scenes is a process that can run in two directions: a back side can be completed from a front view, or vice versa. For this task, according to the above hypothesis, the cortex is particularly well suited since the general format of its output is the same as that of its input. Otherwise cortex could not project to cortex.

A fundamentally different way of processing visual information would be to associate one's own running around an object with first seeing its front side and then the back side, whereas running in the opposite direction shows the sides in reverse order. Then the time delay depends on running, and it is unlikely that the primate-like notion of "the object" could arise from this processing method. Rather, a notion of "type of object" (to which an odor, a taste, a texture, typical noises when touched, and individual experiences may be associated) would be combined to a location, and to the way how to get there.

(5) Differences to Humans

According to the hypotheses presented so far, monkeys have achieved to find a common format for the representation of both visual and (translated) motor signals, and they have set the stage for translating *everything* in the brain to this format. They are specialists of applying visual completion computations to data presented in this format. They do this by making extensive use of the general concatenation capabilities of the cortex, up to the point where excessive processing times introduce problems of time reference.

Finding a solution to the latter problem would clear the way for a quasi unlimited use of cortical processing power, and a corresponding increase of cortical volume, provided that secondary restrictions can be overcome.

The hypothesis is that the *essential* evolutionary step from monkey to man is to have found that solution, which is to introduce the use of time tags that are associated to the excitation patterns to which they refer. These tags are excitation patterns, too, and their significance is "explicit time", or some temporal relationship, such as "yesterday", or "valid for a long time". Upon that invention, indeed a rapid, until now unexplained expansion of the cortex occurred.

Artificial chimpanzee speech, besides other defects, lacks the elements of human language to indicate temporal relationships (see e.g., Pinker, 1994). In this respect, apes seem to be closer to monkeys.

Obviously, if an explicit time tag is used, the old "implicit time rule" of each outer-world event occurring simultaneously with the corresponding neuronal excitations (see above) can no longer be valid.

Therefore, from this evolutionary step on, two types of excitation had to be kept apart. For the ones the implicit time rule was valid, and they were used for online processing. For the others, the times of occurrence were determined by processing needs but had no significance in outer-world terms. The time (or time span) at which such an excitation had an outer-world significance was expressed by an associated time tag. It could point to a time in the past or in the future. The way of handling these excitations corresponds to *offline processing*.

There is more to the two ways of processing than just a difference of treating time: for the first time in cerebral evolution, some kind of "significance" had to be invented to differentiate between the roles of the excitation patterns as they occurred in the offline system, including the (computational) relationships to their predecessors and successors, and their "meaning", i.e., the relationships to predecessors and successors that they would have in the online system even if no such online process was actually run. The important detail of this statement is the absence of a reference to the "outer world".

I have already referred to the example of the object whose back side is deduced from the front view by a completion step, using a retrieval process from an association memory. In the offline system the back side is the *consequence* of the front side. However, the *meaning* of this is is an object in the outer world that has no constituents of which some are the causes, and others the effects.

The hypothesis is that *"perception" is the attribution of an "online meaning" to the result of an offline computation* applied to sensory signals. The most well-known effect of perception is that the time tag "valid for a long time" can be attributed to brief sensory excitation patterns, so that a continuous stable perception of the world can arise.

The question of the scientific nature of this attribution process cannot be addressed here. It may just be noted that the online system produces motor output whose effects are in the outer world, i.e. they are not *identical* with any process occurring in the brain. The offline system produces "meaning" which is not identical, neither, with any process occurring in the brain.

The hypothesis is that the greatest evolutionary pressure for a new way of handling time did not arise from pure visuovisual completion computations but rather from those involving motor acts and aping. Obviously it is an enormous advantage if a long sequence of actions, such as hunting deer, can be completely be time-tagged (for this, one has to attribute the tags while *doing it oneself**) and then be stored in the same way as a "compound view" of an object. This stored knowledge can then be used when one observes a conspecific *beginning* to hunt. The continuation of the action can be completed by a computation which lasts much shorter than the actual online action of hunting. This is true prediction: it does not comprise own reactions to the result of the computation.

It is evident that the mechanisms involved in aping are prerequisites for this procedure, and that, as in aping, the whole offline computation is essentially a sensory affair, with all motor events being included in a translated sensory format. The way out of the offline system has already been prepared in the monkey brain, but this cannot be treated here in detail. The final step must always be the online system which alone is able to directly produce real behaviour.

The hypothesis is that it is a new type of social interaction that humans have evolved by extending the mechanism underlying aping into the time domain, as it has been described above. The most notable new feature is that conspecifics have greatly extended the circumstances under which they can help each other. Here I am not concerned with altruism or egoism, but with the obvious prerequisite for any kind of helping, namely that (in the absence of speech) one must have some prior knowledge of the goal of the conspecific.

Beyond the primitive level of demand to the nervous system, namely to get recoverable traces of experience into its connectivity, the higher-level question is how to generate these traces without actually having to collect that experience. The oldest solution is to inherit the appropriate connectivity.

This is also the oldest basis of helping, present in many animals. Only after many generations such systems can adapt to new situations. A faster way is the ability of some animals to learn their roles in shared tasks which is also a kind of helping. However, both individuals have to be present during the learning phase so that the buildup of the necessary knowledge can only occur under restricted circumstances. These have to be arranged from the very beginning in such a way that the ability to help is the outcome. In contrast, the basis of the corresponding human ability is much wider: by applying the above procedure marked by *, humans can use own experience gathered without the presence of a conspecific, and apply it to cases in which a conspecific takes the role of oneself.

On the same basis, detrimental actions of a conspecific can be prevented. Note that in such contexts tools have not only a value related to their use, but with the appearance of man they also gain a *communicative* value because they greatly facilitate the identification of the nature of an action intended by a conspecific. This may have accelerated the evolution of tool use as well as of language. Finally, what has evolved to be applied to conspecifics might later also have been applied ot oneself, giving rise to consciousness (MacKay, 1977) and intentionality.

It follows from the preceding paragraphs that there is a rule which is not obvious when presented in isolation. It states that there is a *link between the use of markers of explicit time and a new type of social interactions*, namely to predict the actions of a conspecific. The reason for the existence of this link is that the attribution operation marked by * can only be performed on oneself, but not on external temporal processes (such as observing the breaking of a dyke by a flood) because it also contains own motor signals to which oneself has access. In contrast, there is no access to the way how the water organizes the forces it exerts on the dyke.

(6) Nature of the Monkey

The hypothesis is that monkeys depend exclusively on an online-system. They live without consciousness and perception, and yet they can perfectly see and act, in correspondence to the attempts of descriptions as they are usually given by neurophysiologists (see König and Luksch, 1998: this issue, pp. 542–549). They live always in the presence, and yet they can perfectly guide future behaviour by experience accumulated in the past. They have evolved accurate object vision that allows them to exploit visual transformation rules and visual memory so that an object can be represented, and be recognized, by a kind of compound view including visible and hidden parts. The great weight of vision, in turn, gives rise to the ability of monkeys to recognize themselves as being physically similar to their conspecifics. On the basis of this a visual representation of motor acts has been built up, leading to the faculty of aping, and to an extension of the above compound views of objects to include actions that can be applied to them.

The hypothesis is that monkeys did not evolve a solution to the problem of time reference arising from long computation times that may separate the times of occurrence of excitations belonging to visible and completed parts of a scene.

The complement of this hypothesis is that the essential evolutionary step forward towards man is to have solved this problem by creating an offline processing system, using excitation patterns as time tags. This system, for which the monkey's aping ability is a prerequisite, can be accommodated by a cortical system that is largely built according to the same principles as the one of monkeys. The main new feature is on the level of the *significance* of some of the excitations in that system: some of them signify "explicit time".

So far no hypothesis can be offered for the reason of only *one* offline system existing in man. If this system is working on a process, no other offline process can be run simultaneously.

Introspectively this may give rise to confusion because "simultaneously" does not refer to the times that are indicated by the time tags, but it refers to the times of occurrence of excitations in the brain.

If the offline system is busy with one problem, then the hypothesis is that only online processes can continue to operate. This situation arises e.g. while one does difficult mental arithmetics, which can only be done in the offline system. While doing this, humans are said to be in a state of "absent-mindedness" with regard to all other activities except these arithmetics. It is well known that they continue to show a large variety of learned, highly structured sensory and motor activities, such as dressing, eating a meal using cutlery, or walking along a complicated path in a building, switching on lights, and avoiding obstacles. However, they could neither speak, nor understand language, nor think, without prior interruption of the state of absentmindedness, i.e., the interruption of the arithmetics in this example.

The hypothesis is that the remaining human faculties reveal the performance of the isolated online system. Therefore, humans in the state of "absent-mindedness" may be compared to monkeys. This state is not well investigated, possibly because it has been viewed primarily as a state of degraded overall performance. However, an exploration might be worthwile because it might help to get an idea of how it is for a human brain to be the brain of a monkey.

I guess that an absentminded human would learn a typical monkey training task in about the same time as a monkey, e.g. to touch a light whenever it lights up in green colour, but not when the colour is red.

Experimental Approaches

If the description that I have given of the monkey brain should prove incorrect in essential points, I believe that it is still correct in giving an idea of the *minimum* of functional complexity of the monkey brain, and possibly also on the nature of the conceptual entities appearing in it. In particular, when one tries to explain the behaviour on an animal, it is my impression that in the past too much weight has been given to "evolutionary niches" located in the outer world (such as advantages of jumping from tree to tree) but the roles of "neural niches" (such as advantages of gaining access to the processing power of a larger cortex by finding a trick to handle certain conflicts arising from long computing times) are neglected.

Similarly, in neurophysiological investigations of the monkey brain too much weight is given to outer-world circumstances such as sensory stimuli or behavioural parameters. Usually, one tries to specify rigorously the outer world events, and collects the accompanying neural events in an indiscriminate way.

The type of result of the application of this "classical" method might be that some neurons react to stimulus X1 (or the excitations of some other neurons accompany motor act X2) if the attentional state is X3, with X1 to X3 being entities of the outer world, the latter being defined in terms of some trained animal behaviour. The problem with this procedure is that repeated trials of such experiments usually yield variable results. One resorts to averaging techniques, but there is no way to interpret the variations. The problems increase with the size of the investigated brain, and the farther away from the interfaces to the outer world the recordings are taken.

For large brains, the processing of the cerebral signal contents cannot be understood by solely considering the interactions with the interfaces. Rather, a "reverse method" has to be applied in which the point of departure is similar for the experimenter and the animal: at the outset he/she has to be concerned with purely intracerebral operations such as neuronal correlation detection, classification (i.e., "recognition"; Aertsen and Johannesma, 1981; Krüger and Becker, 1991; Becker and Krüger, 1996; Krüger, 1997) and detection of plasticity. When some well-defined (i.e., discriminable, and repeatedly recognizable) neural event is found, the experimenter has to search for correlates to outer world events. Thus, while in both the classical and the reverse method a search of correlations is performed between neural and outer world events, one shifts the variability, in which the most intriguing brain processes are hidden, from the neural to the outer world side. Averaging over different outer world events will not always be applicable but there is the great advantage of the everyday faculty of human observers to detect common aspects in outer world events that at first sight seem different.

It is often objected that this method lacks scientific rigor for two reasons. Firstly outer world parameters would have to be specified, to meet standards of scientific communication (see König and Luksch, 1998: this issue, pp. 542–549). It is true that the *experimental procedure* has to specified, but this can also consist of defining how one selects, and recognizes repeatedly, some spontaneously occurring excitation pattern.

Secondly, when such a selection has been done, it is obvious that it is unlikely that in a second animal a similar pattern is observed, be it for the reason that an excitation with the same significance has a different distribution, or be it that the second animal just does not produce that excitation. A firmly established predictability of some (intracerebral or outer-world) event on the basis of the appearance of the primary excitation pattern can be a solid scientific result even when it is observed in only one animal. Rejecting the scientific value of such findings is equivalent to ignoring the central problem: brain research suffers from an enormous lack of physiological phenomenology. Just as the anatomical entities in the brain have names, thousands of excitation distributions would have to be given names, even if they do not look alike in different animals, and then one has to find out what they mean. It is often forgotten that the animal can organize its life only by organizing the succession of cerebral events; for the animal, "the same situation" is given only when the cerebral events are the same, irrespective of similarities in the outer world.

The role of recognizing a cerebral event is illustrated in the report of Murthy and Fetz (1992). They unexpectedly observed large oscillatory local field potentials (LFPs) in the sensorimotor cortex of a monkey when it retrieved a raisin from the invisible closed fist of the experimenter. Since well-controllable outer world events known to be relevant in this area did not have this effect, *no result at all* would have been obtained if the neural event had not been recognizable by itself.

Together with V. Lamme in Amsterdam we have observed conspicious high-frequency oscillations of up to 70 Hz in area V1 of monkeys, and the outer world correlate was found to be a coloured stimulus but also a negative emotional component (manuscript in preparation). It is unlikely that anyone would have planned a "classical" experiment where such an emotion were systematically generated in an animal, with the goal to study its influence on V1.

The experimenter applying the reverse method must observe similar cerebral events repeatedly. This is difficult for three reasons: Firstly, if there is no way to increase the likelihood of reappearance of a particular neural excitation pattern, one has to wait. Therefore, long-term recording conditions must be available. Secondly, the recognition of a neural pattern is the more reliable, the more individual neural parameters are taken into account. Therefore, multivariate recordings have to be taken. Thirdly, even if many parameters are taken into account, it is still not known how small a fraction of some true neural event one is observing.

On the other hand, there is already progress with respect to data treatment, namely the segmentation of the multivariate data stream, and thereafter, the classification, or recognition, of neural events (Radons *et al.,* 1994; Becker and Krüger, 1996). Unlike a large-amplitude oscillation, the general case of a repeating neural event will not be identifiable by eye.

We have contributed to diminish these difficulties, by having developed long-term multielectrode recording techniques (Krüger, Spatz and Bondar, in preparation), and methods for segmenting and classifying data thereby obtained.

The effect is a beneficial one for the monkeys: Events *within* the brain have to be fixed, i.e. to be re-identified while one has to collect whatever happens in the outer world. Obviously stereotyped stimulation and behaviour are not compatible with the reverse method. Thus, shifting the requirement of strict definition of experimental circumstances from the outer world (including behaviour) to the neural side, the experiments are no less rigorous, in principle, than classical ones, but the animals are less restricted.

Obviously there is a huge gap between the very complex presumed neural constitution of the monkey and the relatively simple experimental measures taken so far to investigate it. The development of a general technique for repeatedly recognizing neural events is only a prerequisite, and even this is still a difficult procedure. However, the choice is clear: If we assume that the monkey's brain is similar to that of man in some important respects, then the expenditures for future experiments on monkeys have to be greatly augmented, with respect to experimental and data evaluation methods as well as to fundamental considerations. If not, it is better to study earthworms.

Aertsen A. M. J. H., Johannesma P. I. M. (1981), The spectro-temporal receptive field: a functional characteristic of auditory neurons. Biol. Cybern. **42,** 133–143.

Becker J. D. and Krüger J. (1996), Recognition of visual stimuli from multiple neuronal activity in monkey visual cortex. Biol. Cybern. **74,** 287–298.

Di Pellegrino G., Fadiga L., Fogassi L., Gallese V. and Rizzolatti G. (1992), Understanding motor events: a neurophysiological study. Exp. Brain Res. **91,** 176–180.

Fuster J. M. (1998), Cellular dynamics of network memory. Z. Naturforsch. **53c,** 670–676.

Gibbon J., Malapani C., Dale C. L. and Gallistel C. R. (1997), Toward a neurobiology of temporal cognition: advances and challenges. Curr. Opinion Neurobiol. **7,** 170–184.

Giurfa M. and Menzel R. (1997), Insect visual perception: complex abilities of simple nervous systems. Curr. Opin. Neurobiol. **7,** 505–513.

Goldman-Rakic P. S. (1987), Circuitry of primate prefrontal cortex and regulation of behavior by representational memory. In: Handbook of Physiology: The Nervous System (Plum F. and Mountcastle V., eds). American Physiological Society, Bethesda, pp. 373–417.

Goldman-Rakic P. S. (1996), The prefrontal landscape: implications of functional architecture for understanding human mentation and the central executive. Philos. Trans. R. Soc. Lond. (Biol.) **351,** 1445–1453.

Hyvärinen J. (1982), The parietal cortex of monkey and man. Studies of Brain Function Vol. **8.** Springer Berlin.

Koch M. (1998), How can adaptive behaviour plasticity be implemented? Z. Naturforsch. **53c,** 593–598.

König P. and Luksch H. (1998), Active sensing – closing multiple loops. Z. Naturforsch. **53c,** 542–549.

Krüger J. (1997), Erkennung neuronaler Erregungsmuster im visuellen Kortex von Affen. Freiburger Universitätsblätter **135** (march), 75–91.

Krüger J. and Becker J. D. (1991), Recognizing the visual stimulus from neuronal discharges. Trends Neurosci. **14,** 282–286.

Krüger J., Bondar I. and Haan H. (1996), Recording from foveal striate cortex while the monkey is looking at the stimulus. In: Neural Networks: Artificial Intelligence and Industrial Applications (Kappen B. and Gielen S., eds.). Springer, Berlin, pp. 33–36.

MacKay D. M. (1977), What determines my choice? In: Cerebral Correlates of Conscious Experience (Buser P. A. and Rougeul-Buser A., eds.). North Holland, Amsterdam, pp. 335–345.

Murthy V. N. and Fetz E. E. (1992), Coherent 25- to 35-Hz oscillations in the sensorimotor cortex of awake behaving monkeys. Proc. Natl. Acad. Sci. USA **89,** 5670–5674.

Pinker S. (1994), The Language Instinct. W. Morrow, New York.

Puccetti R. and Dykes R. W. (1978), Sensory cortex and the mind-brain problem. Behav.Brain Sci. **1,** 337–375.

Radons G., Becker J. D., Dülfer B. and Krüger J. (1994), Analysis, classification and coding of multielectrode spike trains with Hidden Markov Models. Biol. Cybern. **71,** 359–373.

Rizzolatti G.and Arbib M. A. (1998), Language within our grasp. Trends Neurosci. **21,** 188–194.

Roe A. W., Pallas S. L., Kwon Y. H. and Sur M. (1992), Visual projections routed to the auditory pathway in ferrets: receptive fields of visual neurons in primary auditory cortex. J. Neurosci. **12,** 3651–3664.

Sur M. (1993), Cortical specification: microcircuits, perceptual identity, and an overall perspective. Persp. Develop. Neurobiol. **1,** 109–113.

Tovée M. J. (1996), An Introduction to the Visual System. University Press, Cambridge UK.