
Natural Intelligence and Artificial Intelligence: Bridging the Gap between Neurons and Neuro-Imaging to Understand Intelligent Behaviour

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Summary. The brain has been a source of inspiration for artificial intelligence since long. With the advance of modern neuro-imaging techniques we have the opportunity to peek into the active brain in normal human subjects and to measure its activity. At the present, there is a large gap in knowledge linking results about neuronal architecture, activity of single neurons, neuro-imaging studies and human cognitive performance. Bridging this gap is necessary before we can understand the neuronal encoding of human cognition and consciousness and opens the possibility for Brain-Computer Interfaces (BCI). BCI applications aim to interpret neuronal activity in terms of action or intention for action and to use these signals to control external devices, for example to restore motor function after paralysis in stroke patients. Before we will be able to use neuronal activity for BCI-applications in an efficient and reliable way, advanced pattern recognition algorithms have to be developed to classify the noisy signals from the brain. The main challenge for the future will be to understand neuronal information processing to such an extent that we can interpret neuronal activity reliably in terms of cognitive activity of human subjects. This will provide insight in the cognitive abilities of humans and will help to bridge the gap between natural and artificial intelligence.

1 Introduction

In July 2005 the journal *Science* celebrated its 125 years of existence by publishing a series of ten “hard questions”. These questions were posed to set new goals for science: “The pressures of the great, hard questions bend and even break well-established principles, which is what makes science forever self-renewing—and which is what demolishes the nonsensical notion that science’s job will ever be done”. Most of these hard questions were related to major problems in astronomy, physics, neurobiology, and only one problem (“What Are the Limits of Conventional Computing?”) was directly related to Computational Science. Yet, several of the questions, that were posed from the perspective of Neurobiology, are directly related to computer science and

Stan Gielen: *Natural Intelligence and Artificial Intelligence: Bridging the Gap between Neurons and Neuro-Imaging to Understand Intelligent Behaviour*, *Studies in Computational Intelligence (SCI)* **63**, 145–161 (2007)

www.springerlink.com

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artificial/computational intelligence. Questions like “What Is the Biological Basis of Consciousness?”, “How Are Memories Stored and Retrieved?”, and “How Did Cooperative Behavior Evolve?” are equally crucial to computer science, where problems related to autonomous unsupervised decision making and information retrieval in large, complex data bases, and emergent intelligence are at the heart of Computer Science and Artificial/Computational Intelligence. In this chapter, I will shortly address some aspects of the “hard” problems in Neuroscience regarding consciousness, storage and retrieval of information and the evolution of cooperative behaviour. Then I will explain how these questions relate to major problems in the field of artificial/computational intelligence.

Since long, the basic principles of neuronal information processing have served as a source of inspiration for advanced applications in computer science. In this context it is remarkable that after the booming of the neural network hype in the nineteen eighties, the neural network community has become separated in two streams : one community (frequently called artificial neural network, AI or machine learning community) focussed on algorithms for advanced applications in real-world problems. The other community, called the computational neuroscience community, focussed on more-or-less realistic models to describe the behaviour and function of biological neurons and networks of neurons. The development of these two research lines along separated tracks is somewhat surprising and undesirable since these research lines have many problems in common. Examples of fields of common interest are decision making in complex situations with incomplete information, the design of intelligent autonomous agents and advanced data analysis/retrieval. Presumably the most interesting problems of common interest are related to the phenomena of emergent intelligence and consciousness and their implementation in the neural/computer hardware, which belong to the major long-term goals in both computational intelligence and in AI/machine learning. To some extent, the separate evolution of both fields reflects the different implementation (neural wetware versus computer hardware) and the different background of researchers in both communities. The AI/machine learning community has many researchers with a background in computer science or statistical physics, whereas the computational neuroscience has mainly researchers with a background in neurobiology and theoretical physics.

A particular example of a complex problem that is of relevance to both research communities is the topic of Brain-Computer Interfaces (BCI). BCI tries to extract meaningful signals from neuronal signals, among others for the diagnosis and rehabilitation of patients with neurological disorders. This topic deals with many problems that belong to the core of the AI/machine learning community and of the computational neuroscience community. It deals with pattern recognition and classification of highly complex data with a very poor signal to noise ratio. Moreover, the neural code, i.e. the meaning and function of the neuronal signals is hardly known, since we do not know the detailed functional role of various brain structures, nor do we know how information is

encoded in the temporal properties of the parallel distributed pathways and how attention or dysfunction modifies the neuronal signals. A reliable classification of neuronal signals not only requires advanced data-analysis techniques; knowledge about the neural code and about the involvement of neuronal structures in neuronal information processing is equally important for successful BCI applications.

2 Brain Computer Interfaces

Any type of goal-directed behaviour is reflected in a characteristic sequence of neuronal activities in various parts of the brain. In the past decade it has become clear that not only the decision to start a task and the performance of the task (which should be taken very general as it can imply both perceptual tasks as well as motor performance), but even the intention to take action, is reflected in the neuronal activity. In large parts of the human brain the neuronal activity is very similar to that for subjects who intend or plan actions and for subjects, who really perform these actions [25]. This feature is used for BCI applications. A Brain-Computer Interface (BCI) generally aims to provide a communication channel from a human to a computer that directly translates brain activity into sequences of control commands. Such a device may give disabled people direct control over a neuro-prosthesis or over computer applications as tools for communicating solely by their intentions that are reflected in their brain signals (e.g. [27, 26, 53, 3, 38]). The hope is that BCI can possibly reach this goal in the near future by recording brain activity and by using these signals to control a device. For example, this device could be the limb of a subject when the subject is paralysed (for example after a stroke or in case of Amyotrophic Lateral Sclerosis (ALS), which leads to complete paralysis of all muscles for an otherwise intact central nervous system). In that case the recorded brain signals could be used for artificial electrical stimulation of muscles, which leads to muscle contraction and limb movements. BCI tools are thought to become an important tool when normal functioning of the brain (such as after a stroke) is limited.

Not only does BCI address the issue of translating brain activity into control commands, it also deals with interfering with brain activity by electrical stimulation of the brain. At present deep-brain stimulation is used in severe Parkinson patients, when the traditional treatment of patients with Parkinson's disease with levodopa (a drug which replaces the neurotransmitter dopamine which is no longer produced in the basal ganglia in Parkinson Patients) fails. Deep brain stimulation does not provide a cure for Parkinson's Disease, but greatly alleviates the symptoms [18]. Other applications can be found in the sensory domain. The artificial cochlea, which provides hearing to deaf people with a disorder in the peripheral auditory system [5, 6, 21, 54], has become a standard medical treatment. Another application, that is expected

to become equally successful as the “artificial cochlea”, is the “artificial retina” [13, 14, 39].

In most BCI applications (both realised as well as planned applications), brain activity is measured by means of a multi-electrode (typically 128) electroencephalogram (EEG), which is a measure for the weighed activity of many cells in the brain. The temporal resolution of EEG is excellent (typically in the range of a millisecond). The main problem of this technique is the poor signal-to-noise ratio (SNR), which makes it hard to distinguish the location and contribution of multiple sources of activity in a normal functioning brain. The accuracy of source localisation is typically in the order of a centimetre if the number of sources is limited to three, but becomes rather hopeless if more than 5 sources of neuronal activity are involved. High-resolution EEG is non-invasive as opposed to invasive work by e.g. Nicolelis [30, 31] who used implanted electrodes in the brain to record the activity in various brain structures. Sub-dural electrodes have a much better signal-to-noise ratio, but have the disadvantage of being invasive. Non-invasive data acquisition is a requirement for most applications, but has the disadvantage that the signals of interest are ‘hidden’ in a highly ‘noisy’ environment as EEG signals consist of a superposition of a large number of simultaneously active brain sources that are typically distorted by artefacts and even subject to non-stationarity. The non-stationarity is the consequence of modulation of neuronal signals by attention or by competition between multiple sensory stimuli. Moreover, the brain is highly adaptive and can even involve new pathways to compensate for lesions in the brain. An ideal BCI application should be adaptive to the task and the subject and should adapt rapidly. Actually, it should be the algorithm, which adapts itself to the subject, rather than the subject who adapts to the BCI device. Moreover, BCI should have short yield high information transfer rates. Therefore, advanced data-analysis techniques are absolutely necessary.

3 The Neural Code

Traditionally the easiest and most accurate method to measure neuronal activity is to record the action potentials of single neurons. The long tradition of single-unit recording has revealed that information in the brain is coded in firing rate of a neuron (i.e. the number of action potentials per unit of time) and in recruitment: the orderly recruitment of neurons as a function of stimulus intensity or motor output. Single-unit recordings have been very successful and have revealed many secrets about neuronal information processing. However, single-unit recordings are not suitable to measure correlations in neuronal activity of various neurons within a neuronal ensemble. Such correlations might be due to common input or to lateral neuronal interactions. Knowledge about correlations in neuronal activity is important to understand the nature and amount of information that is encoded by an ensemble of neurons. For an ensemble of N neurons the firing rate of this

ensemble to a stimulus s can be represented by the vector \vec{r} with r_j representing the firing rate of neuron j . If the probability for firing rate r_j of neuron j given the stimulus s is $p(r_j|s)$, the information encoded by this ensemble is $I(s) = - \int p(\vec{r}|s) \ln p(\vec{r}|s) d\vec{r}$. If neurons do not have neuronal interactions, such that firing rates are independent, we have $p(\vec{r}|s) = \prod_j p(r_j|s)$, such that the information $I(s)$ can be written as $I(s) = - \sum_j \int p(r_j|s) \ln p(r_j|s) dr_j$. This implies that the information in the activity of the ensemble of neurons is simply the sum of information encoded by each of the neurons. If neuronal information encoded by different neurons is correlated, it is not longer true that $p(\vec{r}|s) = \prod_j p(r_j|s)$. From a theoretical point of view, this would imply that the amount of information encoded by the ensemble of neurons is in general less than the sum of information encoded by the individual neurons (see e.g. [33]). However, since the generation of an action potential is a stochastic process, correlated firing allows elimination of noise by averaging. Therefore, correlated firing may reflect a compromise to obtain optimal information transfer by reducing noise. More detailed information about the information in neuronal ensembles can be found in [42].

In order to explore the temporal correlation between firing of neurons, the next logical step was the development of multi-unit recording techniques by arrays of electrodes. These multi-unit recordings have revealed a third coding mechanism for neuronal information: coding by temporal correlation of action potential firing [9, 47]. At any moment in time, many neurons are active in the brain. Multi-unit recordings have shown that active neurons can be subdivided in subgroups of neurons, where neurons in the same subgroup reveal a high temporal correlation of firing. Microelectrode recordings in monkeys, as well as neuroimaging studies in man have revealed that these ensembles of neurons can (re)organize rapidly and in a flexible way into subgroups, where activity of neurons in the same subgroup reveals a high temporal correlation of firing without changes in mean firing rate (see e.g. [46, 47]). The functional significance of the temporal locking is not known, but there are various hypotheses about its functional significance (see e.g. [44]).

4 Recording Neuronal Signals from the Brain

Each neuron receives spike-input from many other neurons. The input of action potentials to a neuron arrives at the dendrites of the neuron where each action potential induces the release of a specific neurotransmitter. This neurotransmitter opens ion-channels, which allows ions to move through the cell membrane into the neuron. These ion currents cause a local change in the membrane potential (the so-called post-synaptic potential). Changes of the membrane potential of a neuron are the result of the many post-synaptic potentials due to input by action potentials from other neurons. The flow of

these currents from the dendrites to the cell body explains why a neuron can be modelled as a dipole.

Typically a neuron receives input from 10^3 to 10^4 neurons. The amount of synaptic input modulates the strength of the dipole. The EEG activity, recorded on the skin above the skull, reflects the contribution of the many dipoles. If all neurons would receive uncorrelated input, the EEG on the skull would be nothing more than noise. However, the input to ensembles of neighbouring neurons is not uncorrelated. This is particularly true for so called Evoked-Brain potentials, where simultaneous onset of neuronal activity is triggered by the sudden onset of a stimulus. Well-known examples are the EEG activity above visual cortex due to onset of neuronal activity at the presentation of a checkerboard pattern or the evoked potentials in the auditory pathway due to sudden onset of a sound. In addition to these transient components of EEG, the temporal correlation of synchronized neuronal activity is reflected in rapid oscillations in EEG activity. These oscillations have been reported at various frequencies, such as the alpha (8–12 Hz) or theta (5–10 Hz) rhythm and the frequently reported beta (12–28 Hz) and gamma oscillations (29–80 Hz). EEG activity reflects the activity of neurons with a dipole orientation orthogonal to the skull. However, since the cortex folds with various sulci, many neurons have an orientation parallel to the skull, rather than orthogonal. These neurons do not or hardly contribute to EEG activity on the skull. However, the ion currents of the neurons parallel to the skull give rise to tiny magnetic fields with an amplitude smaller than that of the earth magnetic field. These small magnetic field components can be measured using SQUIDS in the so-called magneto-encephalogram (MEG). Therefore, MEG is complementary to EEG. Both reflect neuronal activity, but of different groups of neurons.

Another important measure of neuronal activity is obtained by functional Magnetic Resonance Imaging (fMRI). The metabolism related to neuronal activity causes differences in oxygen consumption. Oxygen is transported through the blood vessels by means of hemoglobin molecules. Hemoglobin with oxygen (oxyhemoglobin) is diamagnetic, whereas deoxyhemoglobin (hemoglobin after release of oxygen) is paramagnetic, causing microscopic magnetic field inhomogeneities that affect the transverse relaxation time (called T_2) of the MRI. Since increased neuronal activity leads to an increased blood flow, actually overcompensating for the neuronal oxygen need, the oxygen concentration increases in the blood vessels. Hence the relaxation time T_2 of brain tissue to a radio pulse, which deflects the atom spins oriented along the major magnetic field, is larger for active neuronal tissue than for neuronal tissue at rest. fMRI measures the magnetic relaxation signal due to the perturbing radio pulse.

EEG and MEG both have a high temporal resolution. The disadvantage is that the inverse problem (the problem of finding the location of the electric or magnetic sources that gave rise to the measured EEG or MEG activity) is an ill-posed problem since many different sources of activity can provide the same

EEG or MEG activity on the skull. Therefore, source estimation (estimating the temporal properties and the location of the electric or magnetic sources) is possible only if prior knowledge is available about the number of sources (which should be limited) or if prior knowledge is available about the position and temporal modulation of the sources. fMRI typically has a high spatial resolution (typically a few tenths of a millimeter). However, the temporal resolution (tenth of a second) is way above a millisecond, which is the time constant to characterise neuronal activity. Therefore, a combination of both techniques is typically used in advanced neuroimaging research.

5 Basic Questions Regarding the Interpretation of Neuronal Oscillations

5.1 Functional Role of Neuronal Oscillations

Although no one will deny the existence of neuronal oscillations nowadays, their functional significance is yet a topic of debate and few hypotheses exist to explain why and how various ensembles of neurons develop in a flexible way, each with a high temporal correlation structure. These two issues are related and reflect two important problems in neuroscience. Understanding the functional role and the origin of synchronized neural activity is crucial for research on neuronal information processing with large implications for BCI. As pointed out before, correlated firing may be a way to obtain more accurate information coding by eliminating noise. However, other hypotheses have been put forward that attribute other functional roles to correlated firing. In order to explain this we will first discuss the various hypotheses about the functional significance (see also [44]) before we discuss the possible neuronal mechanisms that can explain the initiation and disappearance of neuronal oscillations.

The first hypothesis to provide a functional significance to synchronized neuronal activity is that synchronization plays a role in the representation of sensory information. The most well-known example is the hypothetical role to solve the binding problem. Visual information comes from the retina and passes along the LGN (Lateral Geniculate Nucleus) in the thalamus to the visual cortex (V1). After V1, different features of visual information are processed along different parallel channels. Each channel encodes a particular feature of visual objects, such as color, position of the object, nature of object, and object velocity. For a single object in the visual environment, each channel carries information about a single feature of the object. However, since the visual environment contains multiple objects, each channel carries information about features from multiple objects and the question is how the central nervous system knows which feature belongs to which object. For example, if we have a red pencil and a blue coffee cup, how does the brain know that the label “blue” belongs to the coffee cup and not to the pencil. The idea has been proposed (see [47]) that the temporal correlation might serve as a label

for all features that belong to the same object (however, see [45]). Previous work hypothesized that neuronal coherence (or phase-locking or synchronization) could provide a tag that binds those neurons that represent the same perceptual object. This binding tag would be a flexible code for linking neurons into assemblies and thereby would greatly enlarge the representational capacity of a given pool of neurons. In line with this hypothesis, it has been suggested that object features represented by spatially distinct neural assemblies are dynamically linked to a coherent percept by synchronized activity in the gamma range [10]. This hypothesis can explain why information in the brain is processed, transferred, and stored by flexible cell assemblies, defined as distributed networks of neuronal groups that are transiently synchronized by dynamic connections [10, 52]. A particular example of temporal locking is the observation of phase-encoding in hippocampal place cells [35]. When a rodent moves around in a limited area, the phase of firing in the theta-rhythm carries more information about location of the rodent within this space than does firing rate [49].

Another hypothesis is that synchrony enhances the saliency of neural responses. This can be understood from the fact that two action potentials, arriving simultaneously at the dendrites of a neuron are much more effective in eliciting an action potential than two action potentials which arrive with a time interval. This is particularly clear if the neuronal time constant is small, such that the neuron operates as a coincidence detector [23]. Therefore, correlated discharges have a much stronger impact on neuronal populations than temporally disorganized inputs [11, 41]. The regulation of interaction with target neurons by coherent firing has been reported in corticospinal projections from motor cortex to the spinal cord [43]. Thus, the oscillatory activity might serve as a dynamic filter, which selects the salient and significant inputs to the network. Along these lines, similar coherent oscillations have also been reported for recordings in monkey motor cortex (see e.g. [2, 1, 16, 19, 20, 36, 37], who studied the cross-correlation and coherence between local field potentials and neural spike trains in monkey primary motor cortex, and [40]).

5.2 Neuronal Mechanisms for Neuronal Synchronization

The role of tight neuronal synchronization has raised the question how “noisy” neurons are able to fire in close synchrony with millisecond accuracy. The explanation is that the time constant of the neuron can be modified by balanced excitatory and inhibitory input [23]. Changing the amount of balanced excitation and inhibition changes the time constant of the neuron without changes in firing rate of the neuron. This can be understood using a popular, but simplified representation of neuronal dynamics: the leaky integrate-and-fire model. According to this model, the dynamics of the membrane potential of the neuron is given by

$$C \frac{dV(t)}{dt} = -\frac{1}{R}V(t) + \sum_i \{G_i(t) * s_i(t)\}(V(t) - V_i) \quad (1)$$

where C represents the capacitance of the cell membrane, R represents the resistance of the cell membrane, $s_i(t)$ represents the spike input from neuron i , $G_i(t)$ represents the conductance of the synaptic contact between the cell and the input from neuron i , and V_N represents the Nernst potential. The symbol $*$ represents convolution. The neurotransmitter released by an incoming action potential opens ion channels and thereby modifies the local conductance G_i of the post-synaptic membrane. The last term in Eq. (1) represents the synaptic input current. Eq. (1) can also be written as

$$\tau \frac{dV(t)}{dt} = -V(t) + R \sum_i I_i(t) \tag{2}$$

where the resistance R is the resistance of the cell membrane which is modulated by the synaptic input and with $\tau = RC$. A large amount of input implies a large conductance and a small resistance R . Therefore, input affects the time constant τ . Obviously, Eq. (2) clearly explains the name of the leaky integrate-and-fire model. For large values of the time constant τ , the neuron integrates the input until it reaches a threshold (typically near -40 mV). Then, an action potential is generated and the membrane potential is reset to the membrane potential at rest, typically near -70 mV. For small values of τ , the membrane potential decays rapidly to its rest value, such that a small value of τ turns the neuron into a coincidence detector: the neuron only fires an action potential if the input from different neurons arrives within a small time interval. This explains why balanced excitation and inhibition changes the behaviour of the neuron from a (leaky) integrator into a coincidence detector, which fires only for tightly synchronized input. Although this can explain the propagation of synchronized neuronal activity from one brain structure to another [7], it does not explain the initiation of synchronized activity.

As mentioned above, many studies have reported synchronized oscillations between various neuronal ensembles. The amount of temporal synchronization between neuronal ensembles is generally expressed by the coherence function in the frequency domain. The coherence between two signals $x(t)$ and $y(t)$ is defined by

$$\gamma(\omega) = \frac{\langle R_{xy}(\omega) \rangle}{\langle \sqrt{R_{xx}(\omega)} \rangle \langle \sqrt{R_{yy}(\omega)} \rangle} \tag{3}$$

where $\langle \cdot \rangle$ represents ensemble average over many corresponding time segments for $x(t)$ and $y(t)$. $R_{xy}(\omega)$ represents the cross-covariance function between $x(t)$ and $y(t)$ in the frequency domain. Usually, one will find the squared coherence function $|\gamma(\omega)|^2$ in the literature to explore the relation between two signals. This squared coherence is a real-valued function of frequency in the range between 0 and 1. If the signal $y(t)$ can be obtained from the signal $x(t)$ by convolution by a linear system in the absence of noise, the squared coherence has value 1. This value becomes smaller when noise or nonlinearities are involved. The more noise or the more complex (nonlinear) the

relation between $x(t)$ and $y(t)$, the more the squared coherence approaches the lower limit value of zero. This explains why the squared coherence, in addition to the mutual-information, has often been used to explore the relation between input and output of an ensemble of neurons or to explore the similarity between signals in different parts of the brain (see e.g. [29, 17]).

The coherence function $\gamma(\omega)$ has a special property in that it captures the frequency-dependent phase relation between $x(t)$ and $y(t)$ by the complex-valued function $R_{xy}(\omega)$. The variability of the relative phase provides information about the coupling strength between two signals. If two signals are tightly coupled, the variability of relative phase will be small. This property is highly important in neuronal synchronization (see also [7]). Moreover, when information goes from x to y , any time delay Δt will cause a frequency dependent phase shift $\Delta\phi = \omega\Delta t$. One might expect that if one brain structure provides input to another brain structure, the phase difference between synchronized activities in these two brain structures will reflect at least the effect of finite conduction velocity of signals between the two brain structures. These differences can be quite large in the motor system, where signals from motor cortex project to neurons in the spinal cord, approximately one meter away. With a typical axonal conduction velocity of 60 m/s, this gives rise to as pure time delay of $\Delta t = 16$ ms and to a frequency-dependent phase shift of $\omega\Delta t$ (see [43]). Quite remarkably, oscillatory neuronal activity in different parts of the brain appears to be almost synchronous, without significant time delays. Significant time delays should be expected for serial processing in several brain structures due to the conduction velocity of neuronal signals in the brain. The absence of time delays is what one should expect for a highly connected network of neuronal ensembles with multiple feedback loops. Such highly connected networks operate as a functional unit and cannot be separated into a set of subsystems with clear unambiguous causal relationships between these subsystems. This finding argues against the simple view of neuronal information processing as a serial process from sensory cortices to motor cortex, for example in the case of sensory information about position of objects, which is translated into motor commands to grasp an object.

Comparison of the relative phase of synchronized neuronal oscillations in two functionally related parts of the nervous system has suggested that the excitability of neurons is modulated such that excitability is maximal at the time of arrival of periodic oscillatory activity [43]. This is highly remarkable: how can the receiving neurons adjust their excitability such that it is optimal at the time of arrival of the synchronized input? Based on the findings by Schoffelen et al. [43], Fries [12] hypothesized that neuronal communication is mechanistically subserved by neuronal coherence. The idea is that activated neuronal groups oscillate and thereby undergo rhythmic excitability fluctuations that produce temporal windows for communication. A recent modelling study showed that coherence is processed accurately between subsequent groups of neurons [57]. Coherence by coherently oscillating neuronal groups is a requirement for effective interaction, because they ensure that the

communication windows for input and for output at the interacting neuronal groups are open at the same times. A recent study [8] suggested a mechanism for modulation of excitation such that the neuronal excitability is optimal at the arrival of a period synchronized input. Thus, a flexible pattern of coherence defines a flexible communication structure.

6 Interpreting EEG/MEG Data : Reading Out the Brain

Triggered by the increased knowledge about the neuronal information processing in the central nervous system, the past five years have shown an exponential increase in publications on BCI. These publications mainly referred to new algorithms for classification of EEG/MEG signals and for transforming these signals into mechanical or electronic output (for a recent overview see [32]). Although the aim is to use BCI for the human brain, most experimental data have been obtained in animal experiments using neuronal activity recorded invasively in multiple brain areas (see e.g. [30, 31]). Patterns of spike trains and local field potentials from multi-electrode recordings represent astonishingly well imagined or intended movements. As explained before, the spatial resolution of source localisation estimation based on EEG or MEG is rather poor. This causes a great problem in recording the activity in a particular brain structure with non-invasive EEG electrodes in humans. A recent study in epileptic patients using invasive presurgically implanted subdural electrodes over frontal regions [24] has shown a good performance in classification of neuronal activity, suggesting that it would be a good BCI tool. With these patients, it was possible in just one session to differentiate without any training imagination of hand-, tongue-, and mouth movement from the electrocorticogram (ECoG). However, invasive recordings cannot be used in standard clinical applications.

These results have created enormous public interest and hope for a rapid solution to critical clinical problems such as communication in locked-in patients and movement restoration in patients with spinal cord lesions and chronic stroke. Unfortunately, there are many problems that have to be solved and standard clinical use of BCI seems out of the question for the near future (see a recent review by Birbaumer [4]) illustrating the complexity of the problem with great technical and conceptual problems.

Further progress in this field depends on several developments. It will be of great help, if more detailed knowledge will become available on the precise role of various brain structures in normal human perception, action, and decision making. Knowledge about the role of various brain structures in sensori-motor tasks will provide insight in the spatial and temporal properties of activity in the brain. Prior information about the source location will enable the extension of the temporal filtering, which is currently used in BCI-applications, to spatio-temporal filters that act as templates for classifying EEG/MEG signals. This will improve the signal to noise ratio of EEG/MEG signals considerably.

Along these lines, the use of advanced data-analysis tools like multi-taper techniques (see [29, 57]) will be necessary to reduce the signal-to-noise ratio. Moreover, more information about the neuronal code will be necessary. What is the functional role of various rhythms of neuronal activity? How are these rhythms created and what modulates their amplitude? It is well known that synchronization (especially in the β and γ range) depends on attention and expectation [40, 43]. Knowledge of the task-dependent functional role of neuronal oscillations might be useful to extract particular frequency bands in EEG/MEG for BCI applications in particular tasks. A proper interpretation of EEG/MEG patterns will also require a better insight in the plasticity of the brain. Plasticity in the brain takes place on a large range of time scales. Some processes of plasticity develop on a time scale of seconds, whereas other processes, such as the activation of some brain region to compensate for damage or dysfunction in another part of the brain, become effective only after days or weeks. This is particularly important for elderly people, when brain function deteriorates, where good tools to diagnose symptoms of dementia and other neurological pathologies might help to alleviate symptoms and to save expenses by timely and effective treatment.

7 Implications for Artificial/Computational Science

A better understanding of neuronal information processing will have large implications for artificial/computational science and for BCI in particular. Although the emergence of intelligent behaviour will remain one of the mysteries of the human brain for quite a while, there are many other aspects that already have an impact.

One example concerns the design of an autonomous system. How can such a system distinguish irrelevant stimuli from relevant stimuli when operating in a complex environment. The problem is that the sensory input in a normal environment contains a huge amount of information. Detailed processing of all sensory information would require large amounts of time and would prohibit rapid responses to relevant stimuli. This is where attention starts to play a role. If prior knowledge is available about the possible relevance of stimuli, attention might help to focus and select the relevant stimuli to speed up sensory processing. Indeed, attention has been shown to reduce reaction times and a recent study [43] has shown that the attention-related probability for the stimulus is highly correlated to the amount of gamma-activity in the EEG, giving rise to shorter reaction times. Several other studies on neuronal information processing have shown that sensory processing is not just a bottom-up process, driven by peripheral stimuli. Rather, neuronal information processing of sensory stimuli is governed by Bayes' law, which says that the sensory interpretation of neuronal activity is determined both by the log-likelihood of the stimulus given the neuronal activity and by the prior probability for the stimulus [15, 22, 34, 50, 51, 55, 56].

Classical theories of sensory processing view the brain as a passive, stimulus-driven device. By contrast, more recent approaches emphasize the constructive nature of perception, viewing it as an active and highly selective process. Indeed, there is ample evidence that the processing of stimuli is controlled by top-down influences that strongly shape the intrinsic dynamics of thalamocortical networks and constantly create predictions about forthcoming sensory events. Coherence among subthreshold membrane potential fluctuations could be exploited to express selective functional relationships during states of expectancy or attention, and these dynamic patterns could allow the grouping and selection of distributed neuronal responses for further processing. Top-down driven selection and processing of sensory information has become one of the basic concepts in robotics and in multi-agent technology, although the implementation is very different from that in the brain. Without any doubt this is to large extent determined by the differences in hardware/wetware.

But how do groups of neurons communicate? And how do top-down influences modify the communication structure within a range of hundred milliseconds while anatomical connections stay unchanged on that time scale? In very general terms, the dominant model of neuronal communication is that a neuron sends its message (encoded in e.g. firing rate or in the degree of action potential synchronization) down its axons to all neurons to which it is anatomically connected. Those receiving neurons combine (e.g. sum and threshold) all the inputs and send their output to neurons to which they have connections. An important aspect of this model is that both the distribution and the reception of neuronal signals is governed solely by the structure of the anatomical connections, i.e. there is no further communication structure beyond the one imposed by anatomical connectedness. However, cognitive functions require flexibility in the routing of signals through the brain. They require a flexible effective communication structure on top of the anatomical communication structure that is fixed, at least on the time scale at which cognitive demands change.

Fries [12] hypothesized that this effective communication structure is mechanistically implemented by the pattern of coherence among neuronal groups, i.e. the pattern of phase-locking among oscillations in the communicating neuronal groups. As explained before, the key factor in this model is that neuronal communication between two neuronal groups mechanistically depends on coherence between them while the absence of neuronal coherence prevents communication. Although this idea has been proposed as a working hypothesis, which needs firm experimental testing, the idea may be a crucial step to understand the biological basis of consciousness [28]. If we understand the neurobiological basis of consciousness, this may serve as an example for the implementation of “consciousness” in artificial systems. However, the diversity of definitions for consciousness hamper progress on this topic both in neurobiology and in AI.

The main challenge for the near future will be to understand the neuronal code and to understand the role of various brain structures in memory, sensorimotor processing and decision making. It would be a tremendous achievement if this information could be used for successful BCI applications. On a longer time scale, we need to understand how self-organization in the brain results in emergent intelligent behaviour. What are the underlying principles for the autonomous development of intelligence and can we find where and how these processes take place in the brain? If so, could we measure this brain activity for advanced BCI applications? BCI applications so far allow only binary decisions with an information flow of just a few bits per second at best. Will we be able to implement models for emergent intelligence and will we be able to use these models to solve complex real-world problems? This information will be crucially important to develop advanced adaptive algorithms to interpret EEG/MEG activity, which can then be used for the diagnosis and therapy of patients with neurological disorders.

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