

13. NEUROENGINEERING

Sensorimotor-Computer Interfaces

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Abstract

Neuroengineering of sensorimotor rhythm based brain-computer interface (BCI) systems is the process of using engineering techniques to understand, repair, replace, enhance, or otherwise exploit the properties of neural systems, engaged in the representation, planning and execution of volitional movements, for the restoration and augmentation of human function via direct interactions between the nervous system and devices.

This chapter reviews information fundamental for the complete and comprehensive understanding of this complex interdisciplinary research field, namely an overview of the motor system, an overview of recent findings in neuroimaging and electrophysiology studies of the motor cortical anatomy and networks and the engineering approaches used to analyze motor cortical signals and translate they into control signals that computer programs and devices can interpret.

Specifically, the anatomy and physiology of the human motor system, focusing on the brain areas and spinal elements involved in the generation of volitional movements is reviewed. The stage is set then for introducing human prototypical motion attributes, sensorimotor learning and several computational models suggested to explain psychophysical motor phenomena based on the current neurophysiology knowledge.

An introduction to invasive and non-invasive neural recording techniques including functional and structural magnetic resonance imaging (fMRI and sMRI), electrocorticography (ECoG), electroencephalography (EEG), intracortical single unit activity (SU) and multiple unit extracellular recordings, and magnetoencephalography (MEG) is integrated with coverage aimed at elucidating what is known about sensory motor oscillations and brain anatomy that are used to generate control signals for brain actuated devices and alternative communication in BCI. An emphasis is on latest findings in these topics and highlighting what information is accessible at each of the different scales and the levels of activity that are discernible or utilizable for effective control of devices using intentional activation sensorimotor neurons and/or modulation of sensorimotor rhythms and oscillations.

The nature, advantages and drawbacks of various approaches and their suggested function as the neural correlates of various spatiotemporal motion attributes are reviewed. Sections dealing with the signal analysis techniques, translation algorithms and adapting to the brains non-stationary dynamics present the reader with a wide-ranging review of the mathematical and statistical techniques commonly used to extract and classify the bulk of neural information recorded by the various recording techniques and the challenges that are posed for deploying BCI systems for their intended uses, be it alternative communication and control, as assistive technologies, for neurorehabilitation, neurorestoration or replacement or recreation and entertainment among other applications. Lastly, a discussion is presented on the future of the field, highlighting newly emerging research directions and their potential ability to enhance our understanding of the human brain and specifically the human motor system and ultimately how that knowledge may lead to more advanced and intelligent computational systems.

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13 Introduction - Neuroengineering in General

Neuroengineering is defined as the interdisciplinary field of engineering and computational approaches to problems in basic and clinical neurosciences. Thus, education and research in Neuroengineering encompasses the fields of engineering, mathematics and computer science on one hand, and molecular, cellular and systems neurosciences on the other hand. Prominent goals in the field include restoration and augmentation of human function via direct interactions between the nervous system and artificial devices. Much current research is focused on understanding the coding and processing of information in the sensory and motor systems, quantifying how this processing is altered in the pathological state, and how it can be manipulated through interactions with artificial devices including brain-computer interfaces (BCIs) and neuroprostheses.

Although there are many topics that could be covered under neuroengineering umbrella this chapter does not aim to cover them all. A focus is on providing a comprehensive overview of state-of-the-art in technologies and knowledge surrounding the human's motor system. The motor system is extremely complex in term of the functions it performs and the structure underlying the control it provides; however, there is an ever increasing body of knowledge on how it works and is controlled. This has been facilitated by studies of animal models, computational models, electrophysiology and neuroimaging of humans. Another important development which is extending the boundaries of our knowledge about the motor system is the development of brain-computer interface (BCI) technologies that involve intentional modulation of sensorimotor activity through executed as well as imagined movement (motor imagery). BCI research not only opens up a framework for non-muscular communication between humans and computers/machines but offers experimental paradigms for understanding the neuroscience of motor control, testing hypothesis and gaining a detailed insight into motor control from the activity of single neuron, a small population of neurons, networks of neurons and the spatial and spectral relationship across multiple brain regions and networks. This knowledge will undoubtedly lead to better diagnostics for motor related pathologies, better BCIs for assistance and alternative non-muscular communication applications for the physically impaired, better rehabilitation for those capable of regaining lost motor function and better understanding of the brain as a whole.

Relevantly, for the context and scope of this handbook, BCI research will contribute to better gaining a better insight of information processing in the brain resulting in better, more intelligent computational approaches to develop intelligent systems, truly intelligent systems – systems that perceive, reason and act autonomously.

The motor system is often considered to be at the heart of human intelligence, from the ‘motor chauvinist’s point of view the entire purpose of the brain is to produce movement’ [1]. This assertion is based on the following observations about movement:-

1. interaction with the world is only achieved through movement.
2. all communication is mediated via the motor system including speech, sign language, gesture and writing.
3. all sensory and cognitive processes can be considered inputs that determine future motor outputs.

Neuroscientists and researchers focusing on other areas and functions of the brain may refute this suggestion given the fact that many regions related to general intelligence are located throughout the brain and that a single “intelligence center” is unlikely. No single neuroanatomical structure determines general intelligence and different types of brain designs can produce equivalent intellectual performance [2]. Nevertheless, there is no doubt that the motor system is critical to the advancement of human level intelligence and therefore in the context of computational intelligence, this chapter focuses on reviewing studies and methodologies that elucidate some of the aspects we know about sensorimotor systems and how these can be studied. Although the aim of the chapter is not to provide an exhaustive review of the available extensive literature, it does aim to provide insights into key findings using some of the state-of-the-art experimental and methodological approaches deployed in neuroscience and neuroengineering whilst at the same time reviewing methodology that could lead to the development of practical BCIs. BCIs have revealed new ways of studying how the brain learns and adapts, which in turn have helped improve BCI designs and better computational intelligence for adapting the signal processing to the adaptation regime of the brain. One of the key findings in BCI research is that it can trigger plastic changes in different brain areas suggesting that the brain has even greater flexibility than previously thought [3]. These findings

can only serve to improve our understanding of how the brain, the most sophisticated and complex organism in the known universe, functions, undoubtedly leading to better computational systems.

13.1 *Human Motor System*

The human motor system produces action. It controls goal-directed movement by selecting the targets of action, generating a motor plan, and coordinating the generation of forces needed to achieve those objectives. Genes encode a great deal of the information required by the motor system — especially for actions involving locomotion, orientation, exploration, ingestion, defence, aggression, and reproduction — but every individual must learn and remember a great deal of motor information during his or her lifetime. Some of that information rises to conscious awareness, but much of it does not. Here we will focus on the motor system of humans, drawing on information from primates and other mammals, as necessary.

13.1.1 Major components of the motor system

The central nervous system that vertebrates evolved comprises six major components: the spinal cord, Medulla, Pons, Midbrain, Diencephalon and Telencephalon, the last five of which compose the brain. In a different grouping, the hindbrain (Medulla and Pons), the midbrain, and the forebrain (telencephalon plus diencephalon) constitute the brain. Taken together, the midbrain and hindbrain make up the brainstem. All levels of the central nervous system participate in motor control. However, let us take the simple act of reaching to pick up a cup of coffee to illustrate the function of the various components of the motor system (Fig. 13.1).

- **Parietal cortex:** processes visual information and proprioceptive information to compute location of the cup with respect to the hand. Sends this information to the motor cortex
- **Motor cortex:** using the information regarding the location of the cup with respect to the hand, it computes forces that are necessary to move the arm. This computation results in commands that are sent to the brainstem and the spinal cord.
- **Brainstem motor centers:** sends commands to the spinal cord that will maintain the body's balance during the reaching movement.

- **Spinal cord:** Motor neurons send the commands received from the motor cortex and the brainstem to the muscles. During the movement, sensory information from the limb is acquired and transmitted back to the cortex. Reflex pathways ensure stability of the limb.
- **Cerebellum:** This center is important for coordination of multi-joint movements, learning of movements, and maintenance of postural stability.
- **Basal ganglia:** This center is important for learning of movements, stability of movements, initiation of movements, emotional, and motivational aspects of movements.
- **Thalamus:** may be thought of as a kind of switchboard of information. It acts as a relay between a variety of subcortical areas and the cerebral cortex, although recent studies suggest that thalamic function is more selective. The neuronal information processes necessary for motor control are proposed as a network involving the thalamus as a subcortical motor center. The nature of the interconnected tissues of the cerebellum to the multiple motor cortices suggests that the thalamus fulfills a key function in providing the specific channels from the basal ganglia and cerebellum to the cortical motor areas.

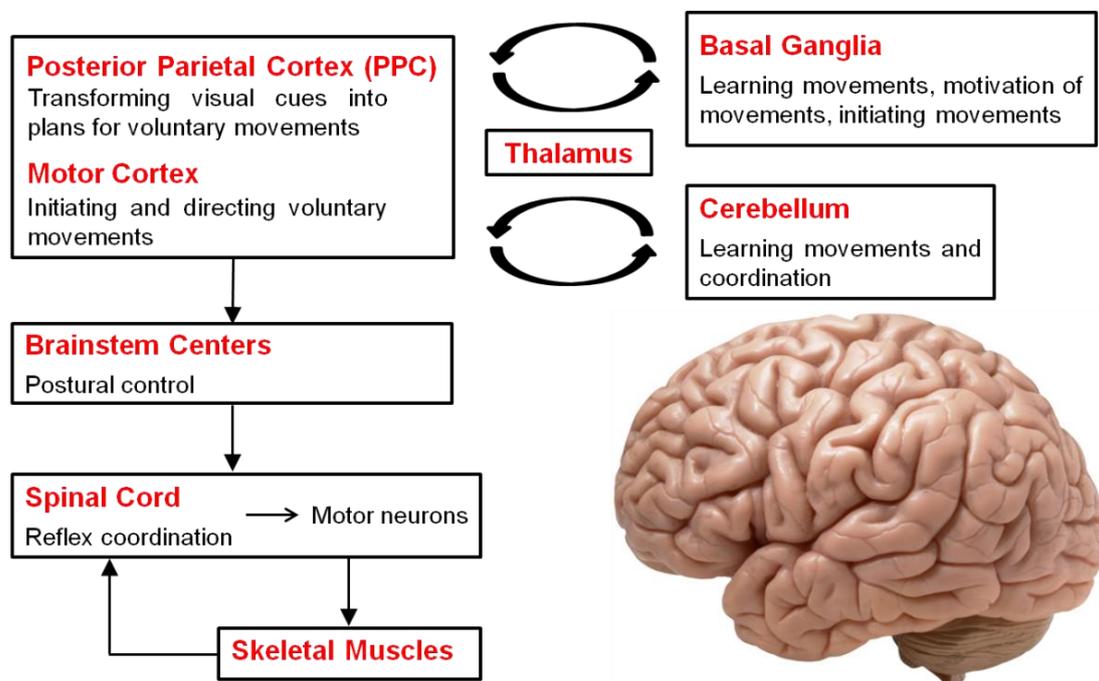


Figure 13.1 Major components of the motor system. (Figure reproduced from <http://www.shadmehrlab.org/Courses/medschoollectures.html> with permission from Reza Shadmehr)

The spinal cord comprises four major divisions. From rostral to caudal, these are called: cervical, thoracic, lumbar, and sacral. Cervix is the Latin word for neck. The cervical spinal segments intervene between the pectoral (or shoulder) girdle and the skull. Thorax means chest (or breast plate). Lumbar refers to the loins. Sacral, the most intriguing name of all refers to some sort of sacred bone.

In mammals, the cervical spinal cord has eight segments; the thoracic spinal cord has 12; and the lumbar and sacral cord both have five. The parts of the spinal cord that receive inputs from and control the muscles of the arms (more generally, forelimbs) and legs (more generally, hind limbs) show enlargements associated with an increasing number and size of neurons and fibers: the cervical enlargement for the arms and the lumbar enlargement for the legs. Each segment is labelled and numbered according to its order, from rostral to caudal, within each general region of spinal cord. Thus, the first cervical segment is abbreviated C1 and together the eight cervical segments can be designated as C1–C8.

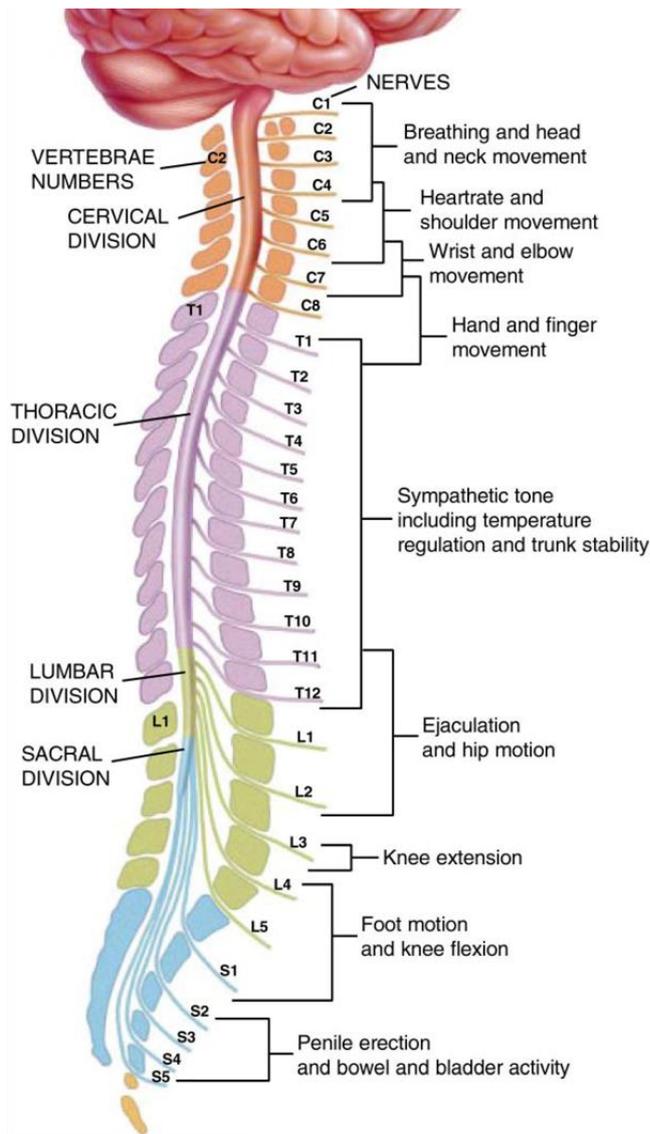


Figure 13.2 Divisions of the spinal cord. (Figure reproduced from <http://www.shadmehrlab.org/Courses/medschoollectures.html> with permission from Reza Shadmehr and John McDonald [4]).

In each spinal segment, one finds a ring of white matter surrounding a central core of gray matter. White matter is so called because the high concentration of myelin in the fiber pathways gives them a lighter, shiny appearance relative to regions with many cell bodies. The spinal gray matter bulges at the dorsal and ventral surfaces to form the dorsal horn and ventral horn, respectively.

The cord has two major systems of neurons: descending and ascending. In the descending group, the neurons control both smooth muscles of the internal organs and the striated muscles attached to our bones. The descending pathway begins in the brain, which sends electrical signals to specific segments in the cord. Motor

neurons in those segments then convey the impulses towards their destinations outside the cord.

The ascending group is the sensory pathways, sending sensory signals received from the limbs and muscles and our organs to specific segments of the cord and to the brain. These signals originate with specialized transducer cells, such as cells in the skin that detect pressure. The cell bodies of the neurons are in a gray, butterfly shaped region of the cord (gray matter). The ascending and descending axon fibers travel in a surrounding area known as the white matter. It's called white matter because the axons are wrapped in myelin, a white electrically insulating material.

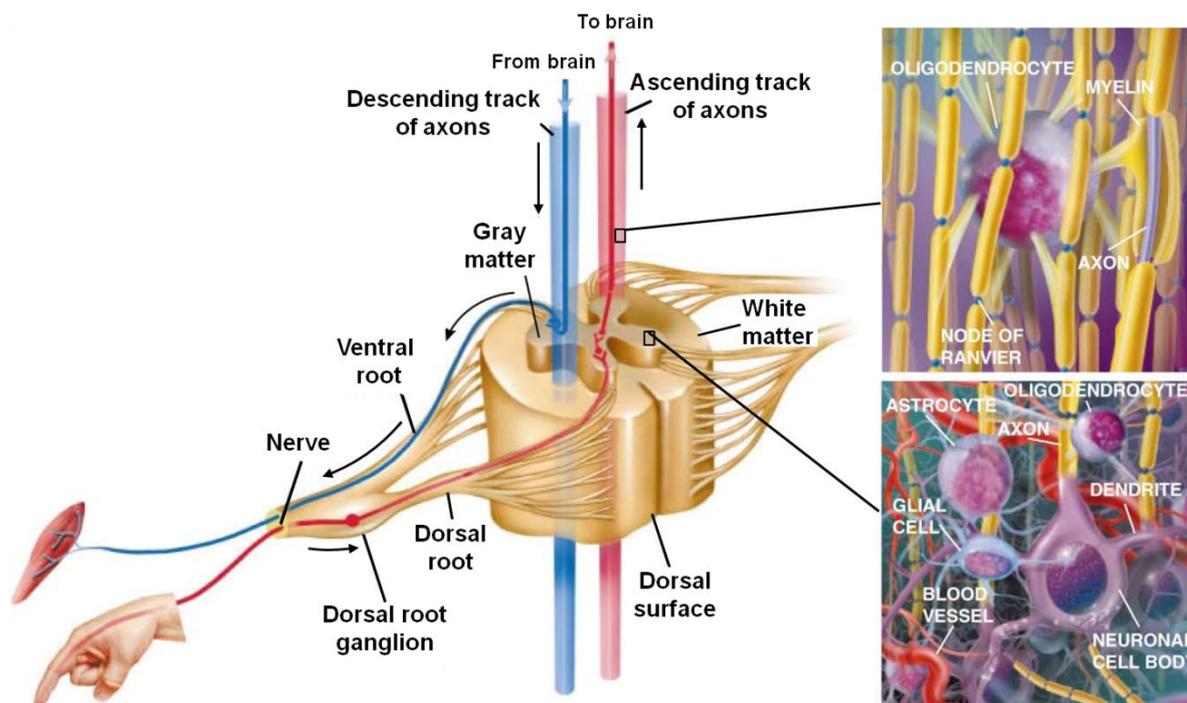


Figure 13.3 A spinal segment. (Figure reproduced from <http://www.shadmehrlab.org/Courses/medschoollectures.html> with permission from Reza Shadmehr and John McDonald [4]).

13.2 Human Motor Control

Motor control is a complex process that involves the brain, muscles, limbs, and often external objects. It underlies motion, balance, stability, coordination, and our interaction with others and technology. The general mission of the human motor control research field is to understand the physiology of normal human voluntary movement and the pathophysiology of different movement disorders. Some of the opening questions include: how do we select our actions of the many actions

possible? How are these behaviours sequenced for appropriate order and timing between them? How does perception integrate with motor control? And how are perceptual-motor skills acquired?

In the following section the basic aspects of motor control - motor planning and motor execution are presented.

13.2.1 Motion Planning and Execution in Humans

Human goal-directed arm movements are fast, accurate and can compensate for various dynamic loads exerted by the environment. These movements exhibit remarkable invariant properties, although a motor goal can be achieved using different combinations of elementary movements.

Models of goal-directed human arm movements can be divided into two major groups: feedback and feed-forward. Feedback schemes for motion planning assume that the motion is generated through a feedback control law whereas feed-forward schemes of trajectory formation propose that the movement is planned in advance and then executed. While a comprehensive model of human arm movements should include feed-forward as well as feedback control mechanisms, pure feedback control mechanisms cannot account for the fast and smooth movements performed by adult humans. Although none of the existing models are able to account for all the characteristics of human motion, there is compelling evidence that mechanisms for feed forward motion planning exist within the CNS. A further supporting argument for the existence of a pre-planned trajectory is that visually directed movements are characterized by relatively long reaction times (RT) of 200 – 500 ms[5], which are supposed to reflect the time needed to plan an adequate movement. A partial knowledge of either the amplitude or the direction of the upcoming movement can significantly reduce the RT.

13.2.2 Coordinate Systems Used to Acquire a New Internal Model

In reaching for objects around us, neural processing transforms visuospatial information about target location into motor commands to specify muscle forces and joint motions that are involved in moving the hand to the desired location[6]. In planar reaching movements, extent and direction have different variable errors, suggesting that the CNS plans the movement amplitude and direction independently and that the hand paths are initially planned in vectorial coordinates without taking into account joint motions. In this framework, the movement vector is specified as an

extent and direction from the initial hand position. Kinematic accuracy depends on learning a scaling factor from errors in extent and reference axes from errors in direction and the learning of new reference axes shows limited generalization[7]. Altogether, these findings suggest that motor planning takes place in extrinsic, hand-centered, visually perceived coordinates. Finally however, vectorial information needs to be converted into muscle forces for the desired movement to be produced. This transformation needs to take into account the biomechanical properties of the moving arm, notably the interaction torques produced at all the joints by the motion of all limb segments. For multi-joint arms, there are significant inertial dynamic interactions between the moving skeletal segments, and several muscles pull across more than one joint. Clearly, these complexities raise complicated control problems since one needs to overcome or solve the inverse dynamics problem. The capacity to anticipate the dynamic effects is understood to depend on learning an internal model of musculoskeletal dynamics and other forces acting on the limb.

The equilibrium trajectory hypothesis for multi-joint arm motions[8] circumvented the complex dynamic problem mentioned above by using the spring-like properties of muscles and stating that multi-joint arm movements are generated by gradually shifting the hand equilibrium positions defined by the neuromuscular activity. The magnitude of the force exerted on the arm, at any time, depends on the difference between the actual and equilibrium hand positions and the stiffness and viscosity about the equilibrium position.

Neuropsychological studies indicated that for M1 (primary motor) region, the representations that mediate motor behaviour are distributed, often in a graded manner, across extensive, overlapping cortical regions, so that different memory systems could underlie different coordinate systems, which are used at different hierarchical levels.

13.2.3 Spatial Accuracy and Reproducibility

Our ability to generate accurate and appropriate motor behaviour relies on tailoring our motor commands to the prevailing movement context. This context embodies parameters of both our own motor system, such as the level of muscle fatigue, and the outside world, such as the weight of a bottle to be lifted. As the consequence of a given motor command depends on the current context, the CNS has to estimate this context so that the motor commands can be appropriately

adjusted to attain accurate control. A current context can be estimated by integrating two sources of information: sensory feedback and knowledge about how the context is likely to have changed from the previous estimate. In the absence of sensory feedback about the context, the CNS is able to extrapolate the likely evolution of the context without requiring awareness that the context is changing[9].

Although the CNS tries to maximize our motion accuracy, systematic directional errors are still found. These errors may result from a number of sources. One cause for not being accurate is a visual distortion, which could be the outcome of eyes fatigue or inherent optical distortion. A second cause could be imperfect control processes due to the noise in the neuromuscular system or blood flow pulsations, which cause our movements to be jerky. A third cause could be that each movement we utilize, consciously or unconsciously, may involve different motor plans, which result in slightly different trajectories and endpoint accuracies.

In a simple aiming movement, the task is to minimize the final error, as measured by the variance about the target. The endpoint variability has an ellipsoid shape with two main axes perpendicular one to another. This finding has led to the vectorial planning hypotheses stating that planning of visually guided reaches is accomplished by independent specification of extent and direction[7]. It was later suggested that the aim of the optimal control strategy is to minimize the volume of the ellipsoid, thereby being as accurate as possible. Non-smooth movements require increased motor commands, which generate increased noise; smoothness thereby leads to increased end-point accuracy but is not a goal in its own. Although the end-point-error cost function specifies the optimal movement, how one approaches this optimum for novel, unrehearsed movements is an open question.

13.3 Modelling the Motor System – Internal Motor Models

An internal model is a postulated neural process that simulates the response of the motor system in order to estimate the outcome of a motor command. The internal model theory of motor control argues that the motor system is controlled by the constant interactions of the “plant” and the “controller.” The plant is the body part being controlled, while the internal model itself is considered part of the controller. Information from the controller, such as information from the CNS, feedback information, and the efference copy, is sent to the plant which moves accordingly.

Internal models can be controlled through either feed-forward or feedback control. Feed-forward control computes its input into a system using only the current state and its model of the system. It does not use feedback, so it cannot correct for errors in its control. In feedback control, some of the output of the system can be fed back into the system's input, and the system is then able to make adjustments or compensate for errors from its desired output. Two primary types of internal models have been proposed: forward models and inverse models. In simulations, models can be combined together to solve more complex movement tasks.

The following section elaborates on the two internal models, introduces the concept of optimization principles and its use in modelling human motor behaviour, presenting a well-established motor control model for 2D volitional hand movement.

13.3.1 Forward Models, Inverse Models and Combined Models

In their simplest form, forward models take the input of a motor command to the "plant" and output a predicted position of the body. The motor command input to the forward model can be an efference copy. The output from that forward model, the predicted position of the body, is then compared with the actual position of the body. The actual and predicted position of the body may differ due to noise introduced into the system by either internal (e.g. body sensors are not perfect, sensory noise) or external (e.g. unpredictable forces from outside the body) sources. If the actual and predicted body positions differ, the difference can be fed back as an input into the entire system again so that an adjusted set of motor commands can be formed to create a more accurate movement.

Inverse models use the desired and actual position of the body as inputs to estimate the necessary motor commands which would transform the current position into the desired one. For example, in an arm reaching task, the desired position (or a trajectory of consecutive positions) of the arm is input into the postulated inverse model, and the inverse model generates the motor commands needed to control the arm and bring it into this desired configuration.

Theoretical work has shown that in models of motor control, when inverse models are used in combination with a forward model, the efference copy of the motor command output from the inverse model can be used as an input to a forward model for further predictions. For example if, in addition to reaching with the arm, the hand must be controlled to grab an object, an efference copy of the arm motor command

can be input into a forward model to estimate the arm's predicted trajectory. With this information, the controller can then generate the appropriate motor command telling the hand to grab the object. It has been proposed that if they exist, this combination of inverse and forward models would allow the CNS to take a desired action (reach with the arm), accurately control the reach and then accurately control the hand to grip an object.

13.3.2 Adaptive Control Theory

With the assumption that new models can be acquired and pre-existing models can be updated, the efference copy is important for the adaptive control of a movement task. Throughout the duration of a motor task, an efference copy is fed into a forward model known as a dynamics predictor whose output allows prediction of the motor output. When applying adaptive control theory techniques to motor control, the efference copy is used in indirect control schemes as the input to the reference model.

13.3.3 Optimization Principles

Optimization theory is a valuable integrative and predictive tool for studying the interaction between the many complex factors, which result in the generation of goal-directed motor behaviour. It provides a convenient way to formulate a model of the underlying neural computations without requiring specific details on the way those computations are carried out. The components of optimization problems are: a task goal (defined mathematically by a performance criterion or a cost function), a system to be controlled (a set of system variables that are available for modulation) and an algorithm capable of finding an analytical or a numerical solution. By rephrasing the learning problem within the framework of an optimization problem, one is forced to make explicit, quantitative hypothesis about the goals of motor actions and to articulate how these goals relate to observable behaviour.

As indicated in the last section, goal-directed arm movements exhibit remarkable invariant properties despite the fact that a given point in space can be reached through an infinite number of spatial, articular, and muscle combinations. In order to account for this observation it is necessary to postulate the existence of a “regulator”, i.e., a functional constraint, to reduce the number of degrees of freedom available to perform the task. Most of the regulators proposed during the last decade refer to a general hypothesis that the nervous system “tries” to minimize some cost related to

the movement performance. Nelson[10] first formulated this idea in an operative way by proposing to use mathematical cost functions to estimate the energy or other costs consumed during a movement. This approach was further developed by several investigators who proposed different criteria such as, for instance, the minimum muscular energy, the minimum effort, the minimum torque, the minimum work or the minimum variance. A model that is indisputably one of the most mentioned in the literature and has proven to be very powerful in describing multi-joint movements is the minimum jerk model described in the next section.

13.3.4 Kinematic Features of Human Hand Movements and the Minimum Jerk Hypothesis

Human point-to-point arm movements restricted in the horizontal plane tend to be straight, smooth, with single-peaked, bell-shaped velocity profiles and are invariant with respect to rotation, translation and spatial or temporal scaling. Motor adaptation studies in which unexpected static loads or velocity-dependent force fields were applied during horizontal reaching movements further supported the hypothesis that arm trajectories follow a kinematic plan formulated in extrinsic Cartesian task-space. The morphological invariance of the movement in Cartesian space supported the hypothesis that the hand trajectory in task-space is the primary variable computed during movement planning. It is assumed that following the planning process, the CNS performs the nonlinear inverse kinematics computations, which convert time sequences of hand position into time sequences of joint positions.

The kinematic features of one-joint goal directed movements were successfully modelled by the minimum jerk hypothesis[11] and were later extended for planar hand motion[12]. The minimum jerk model states that the time integral of the squared magnitude of the first derivative of the Cartesian hand acceleration (jerk) is minimized.

$$C = \int_0^T \left(\frac{d^3 r}{dt^3} \right)^2 dt \quad (13.1)$$

where $r(t) = (x(t), y(t))$ are the Cartesian coordinates of the hand and T is the movement duration. The solution of this variational problem, assuming zero velocity and zero acceleration at the initial and final hand locations r_i, r_f , is given by

$$r(t) = r_i + \left(10 \left(\frac{t}{T} \right)^3 - 15 \left(\frac{t}{T} \right)^4 + 6 \left(\frac{t}{T} \right)^5 \right) (r_f - r_i) \quad (13.2)$$

The experimental setup and the comparison between experimental data and the minimum-jerk model prediction for hand paths, tangential velocities, and acceleration components between different targets are depicted in Fig. 13.4.

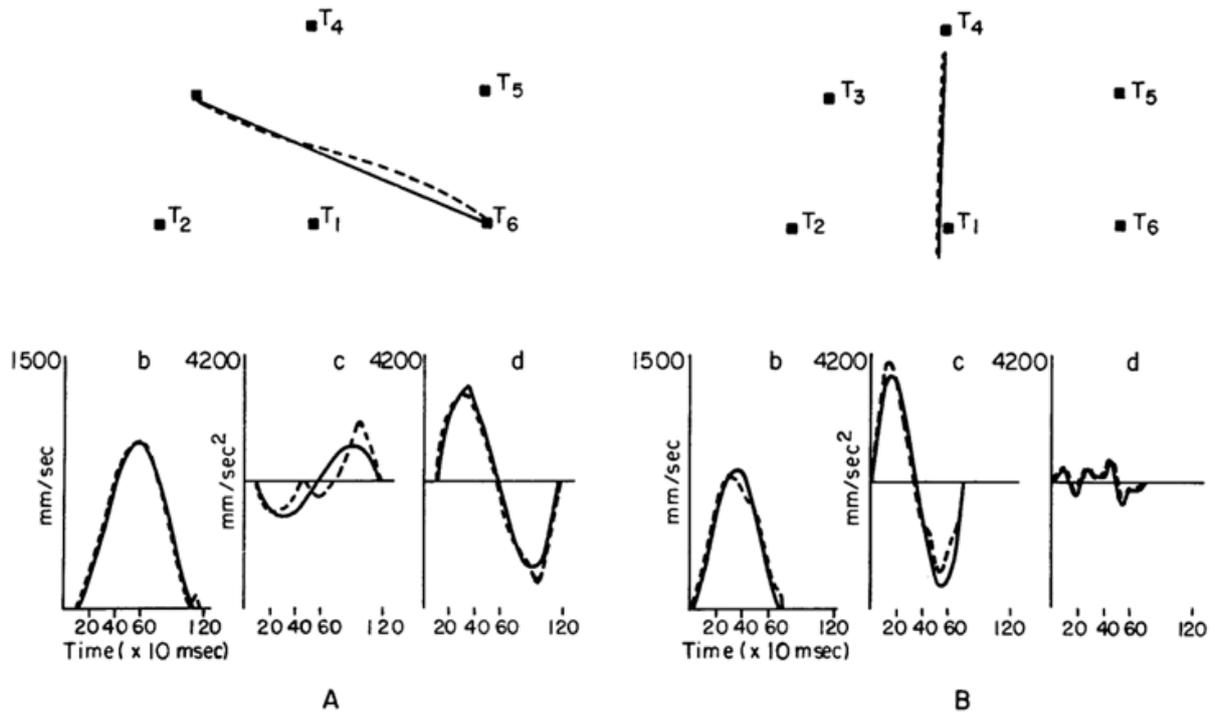


Figure 13.4 Overlapped predicted (solid lines) and measured (dashed lines) hand paths (a), speeds (b), and acceleration components along the y-axis (c) and along the x-axis (d) for two unconstrained point-to-point movements. **A** A movement between targets 3 and 6. **B** A movement between targets 1 and 4 (Figure reproduced from [12] with permission from Tamar Flash).

13.3.5 The Minimum Jerk Model, Target Switching Paradigm and Writing-like Sequence Movements

The stereotyped kinematic patterns of planar reaching movements are not the expression of a pre-wired or inborn motor pattern, but the result of learning during ontogenesis. When infants start to reach, their reaching is characterized by multiple accelerations and decelerations of the hand, while experienced infants reach with much straighter hand paths and with a single smooth acceleration and deceleration of the hand. It is possible to decompose a large proportion of infant reaches into an underlying sequence of submovements that resemble simple movements of adults. It is now believed that the CNS uses small, smooth sub movements, commonly known

as "motion primitives", which are smoothly concatenated in time and space, in order to construct more complicated trajectories. Motor primitives can be considered neural control modules that can be flexibly combined to generate a large repertoire of behaviours. A primitive may represent the temporal profile of a particular muscle activity ("low level", dynamic intrinsic primitive) or a geometrical shape in visually perceived Cartesian coordinates ("high level", kinematic extrinsic primitive[13][14]). The overall motor output will be the sum of all primitives, weighted by the level of activations of each module. A behaviour for which the motor system has many primitives will be easy to learn, whereas a behaviour that cannot be approximated by any set of primitives would be impossible to learn[15].

The biological plausibility of the "primitives' modules" model was demonstrated in studies on spinalised frogs and rats that showed that the Premotor circuits within the spinal cord are organized into a set of discrete modules[16]. Each module, when activated, induces a specific force field and the simultaneous activation of multiple modules leads to the vectorial combination of the corresponding fields. Other evidence for the existence of primitive sub-movements came from works on hemiplegic stroke patients which showed that the patients' first movements were clearly segmented and exhibited a remarkably invariant speed vs. time profile.

The concept of superposition was further elaborated and modelled for target switching experiments [17]. It was found that arm trajectory modification in a double target displacement paradigm involves the vectorial summation of two independent plans, each coding for a maximally smooth point-to-point trajectory. The first plan is the initial unmodified plan for moving between the initial hand position and the first target location. The second plan is a time-shifted trajectory plan that starts and ends at rest and has the same amplitude and kinematic form as a simple point-to-point movement between the first and second target locations.

The minimum jerk model is also a powerful model for predicting the generated trajectory when subjects are instructed to generate continuous movements from one target to another through an intermediate target. It was also shown that, using the minimum jerk model, human handwriting properties can be faithfully reconstructed while specifying the velocities and the positions at via-points, taken at maximum curvature locations.

Understanding primitives may only be achieved by investigating the neural correlates of sensorimotor learning and control. We already know a lot about the

neural correlates of motor imagery and execution as highlighted in sections 13.6 and 13.7 which may provide a good starting point to investigate motion primitives but we will have to go beyond basic correlates to understand the time dependent non-linear relationship among various neural correlates of motor learning and control. This will involve new experimental paradigms and computational methods. The following section overviews investigations into sensorimotor learning.

13.4 Sensorimotor Learning

Motion planning strategies may also change with learning. If a task is performed for the first time the only strategy the CNS might follow is to develop a plan, which allows the execution of the task without taking into account the “computational cost”. A repetitive performance might result in a change in the coding of the movement and producing a more optimal behaviour – at a lower computational cost. Thus, practice – the track for perfection, allows the performance of many tasks to improve, throughout life, with repetitions.

Even in adulthood simple tasks such as reaching towards a target or rapidly and accurately tapping a short sequence of finger movements, which appear when mastered to be effortlessly performed, often require extensive training before skilled performance develops. A performance-gain asymptotes after a long training period and is usually kept intact for years to come. Many studies have focused on different aspects of motor learning: time scale in motor learning and development, task and effector specificity, effect of attention and intention and explicit vs. implicit motor learning. These topics are discussed in the next section in the context of motor sequence learning.

13.4.1 Explicit vs. Implicit Motor Learning

When considering sequence learning one needs to distinguish between explicit and implicit learning. Explicit learning is frequently assumed to be similar to the processes which operate during conscious problem-solving, and includes: conscious attempts to construct a representation of the task; directed search of memory for similar or analogous task relevant information; and conscious attempts to derive and test hypotheses related to the structure of the task. This type of learning has been distinguished from alternative models of learning, termed “implicit” learning. The term “implicit” learning denotes learning phenomena in which more or less complex structures are reflected in behaviour although the learners are unable to verbally

describe these structures. Numerous studies have examined implicit learning of serial-order information using the serial reaction time (SRT) task. In this task, learning is revealed as a decrease in reaction times for stimuli presented when needed to repeat a sequence versus those presented in a random order.

There is a vast literature debating what is really learned in the SRT task. The description of a given sequence structure is from a theoretical point of view not trivial because a given structure typically has several different structural components. Implicit learning may depend on each of these structural components. In sequence learning tasks these components may pertain to: Frequency-based, statistical structures (i.e., redundancy), relational structures and temporal and spatial patterns. A literature review shows that all of these components have an influence on the rate in which a sequence is learned.

Neuropsychological research suggests that implicit sequence learning in the SRT task is spared in patients with organic amnesia, so implicit SRT learning does not appear to depend on the medial temporal and diencephalic brain regions that are critical for explicit memory. Conversely, patients with Huntington or Parkinson diseases have consistently shown SRT impairments, so the basal ganglia seem to be critically involved in SRT learning. Recent studies indicate that the anterior striatum affects learning of new sequences while the posterior striatum is engaged in recalling of a well-learned sequence. In the following section the discussion is restricted to explicit motor learning.

13.4.2 Time Phases in Motor Learning

It is reasonable to assume that a gain in a motor performance reflects a change in brain processing which is triggered by practice. The verity that many skills, when acquired, are retained over long time intervals suggests that training can induce long-lasting neural changes. Previous results from neuroimaging studies in which performance was modified over time have shown that different learning stages can be defined by altered brain activations patterns. As an effect of repetition or practice, several studies report that specific brain areas showed increase in the magnitude or extent of activation. Motor skill learning (e.g., sequential finger opposition task) requires prolonged training times and has two distinct phases, analogous to those subserving perceptual skill learning: an initial, fast improvement phase (“fast learning”) in which the extent of activation in M1 area decreases (habituation-like

response) and a slowly evolving, post training incremental performance gains (“slow learning”), in which the activation in M1 increases compared to control conditions[18].

13.4.3 Effector Dependency

Another fascinating enigma in the realm of motor learning is whether the representation of procedural memory in the brain changes throughout training and whether different neural correlates underlie the different learning stages. A study conducted on monkeys in which a sequence of ten button presses is learned by trial and error, has shown that the time course of improvement of two performance measures: key press errors and reaction-time (RT), was different [19]. The key press errors reached an asymptote within a shorter period of training compared to the RTs, which continued to decrease throughout a longer time period. This finding suggested that the acquisition of sequence knowledge (as measured by key press errors) may take place quickly but long-term motor sequence learning (as measured by RT) may take longer to be established, thus different aspects of the task are learned in different time scales. Further studies in monkeys and in humans demonstrated that although effector dependent and independent learning occur simultaneously, effector dependent representation might take longer to establish than effector independent representation.

13.4.4 Coarticulation

After a motor sequence is extensively trained, most of the subjects undergo implicit or explicit anticipation, which results in a coarticulation – the spatial and temporal overlap of adjacent articulatory activities. It is well known that as we learn to speak, our speech becomes smooth and fluent. Coarticulation in speech production is a phenomenon in which the articulator movements for a given speech sound vary systematically with the surrounding sounds and their associated movements. Several models have tried to predict the movements of fleshy tissue points on the tongue, lips, and jaw during speech production. Coarticulation was also studied in hand motor sequence. It was shown that pianists could anticipate a couple of notes before playing, which resulted in hand and finger kinematic divergence (assuming an “anticipatory” position) prior to the depression of the last common note. Such a divergence implies an anticipatory modification of sequential movements of the hand, akin to the phenomenon of coarticulation in speech. Moreover, studies on

fluent finger spelling has shown that rather than simply an interaction whereby a preceding movement affects the one following; the anticipated movement in a sequence could systematically affect the one preceding it.

13.4.5 Movement Cuing

Another important aspect of motor sequence performance is the type of movement cuing, being external or internal. As internally cued movements are initiated at subject's will, they have, by definition, predictable timing. Externally triggered movements are performed in response to 'go' signals; hence, they have unpredictable timing (unless the timing of the 'go' signal is not random and follows some temporal pattern which can be learned implicitly or explicitly). Studies on movement cuing in animals and patients with movement disorders have showed that the basal ganglia are presumably internal-cue generators and that they are preferentially connected with the supplementary motor area (SMA), an area concerned more with internal than with external motor initiation. In normal subjects the type of movement cuing influences movement execution and performance. It has also been shown that teaching Parkinson Disease (PD) patients, who are impaired at tasks involving the spontaneous generation of appropriate strategies, to initiate movements concurrently with external cue improved their motor performance.

The preceding sections have provided a brief overview of the extensive literature available on understanding the motor system from an experimental psychophysics and model based perspective. A focus on general high level modelling is critical to understanding motor control; however, the problem is being tackled from other perspectives, namely understanding the details of neuro and electrophysiology of brain regions and neural pathways involved in controlling motor function. In the context of developing brain-computer interfaces there has been significant efforts focused on understanding small network populations and structural, functional and electrophysiological correlates of motor functions using epidural and subdural recordings as well as non-invasively recorded electroencephalography (EEG), magnetoencephalography (MEG) and magnetic resonance imaging (MRI) based technologies. Understanding the differences between imagined movement and motor execution as well as the effects of movement feedback and no feedback have shed light on motor functioning. The following sections provided a snapshot of some recent findings.

13.5 MRI and the Motor System - Structure and Function

A new key phase of research is beginning to investigate how functional networks relate to structural networks, with emphasis on how distributed brain areas communicate with each other [20]. Structural methods have been powerful in indicating when and where changes occur in both grey and white matter with learning and recovery[21] and disease [22]. Here we review some of the findings in sensorimotor systems with an emphasis on elucidating regions engaged in motor execution and motor imagery (imagined movement) and motor sequence learning.

Even with identical practice, no two individuals are able to reach the same level of performance on a motor skill – nor do they follow the same trajectory of improvement as they learn [23]. These differences are related to brain structure and function but individual differences in structure have rarely been explored. Studies have shown individual differences in white matter (WM) supporting visuospatial attention, motor cortical connectivity through the Corpus Callosum and connectivity between the motor regions of the cerebellum and motor cortex. Steele et al. [23] have studied the structural characteristics of the brain regions that are functionally engaged in motor sequence performance along with the fibre pathways involved. Using diffusion tensor imaging (DTI), probabilistic tractography and voxel based morphometry they aimed to determine the structural correlates of skilled motor performance. DTI is used to assess white matter integrity and perform probabilistic tractography.

Fractional anisotropy (FA) is affected by WM properties including axon myelination, diameter, and packing density. Differences in these properties could lead to the individual differences in performance through pre-existing differences or training-induced changes in axon conduction velocity and synaptic synchronization, or density of innervation [23][24]. Greater fiber integrity along the superior longitudinal fasciculus (SLF) would be consistent with the idea that greater myelination observed in relation to performance may underlie enhancements in synchronized activity between task-relevant regions.

Voxel based morphometry is used to assess grey matter (GM) volume. Individual differences in GM volume could be influenced by multiple factors such as neuronal and glial cell density, synaptic density, vascular architecture, and cortical thickness[25].

The majority of structural studies of individual differences find that better performance is associated with higher fractional anisotropy (FA) or greater GM volume. Individual differences in structural measures reflect differences in the microstructural organization of tissue related to task performance. Greater FA, an index of fiber integrity, may represent a greater ability for neurons in connected regions to communicate. Steele et al. [23] found enhanced synchronization performance on a temporal motor sequence task related to greater fiber integrity of the superior longitudinal fasciculus (SLF) where the rate of improvement on synchronization was positively correlated with GM volume in Cerebellar lobules HVI and V—regions that showed training-related decreases in activity in the same sample. Synchronization performance on the task was negatively correlated with FA in white matter (WM) underlying bilateral sensorimotor cortex, in particular within bilateral corticospinal tract (CST), such that participants with greater final synchronization performance on the tasks had lower FA in these clusters.

The results provide clear evidence of the importance of structure in learning skilled tasks and that a larger corticospinal tract does not necessarily mean better performance. Enhanced fiber integrity in the SLF could result in reduced FA in regions where it crosses the CST and therefore there is a trade-off between the two in the region of the CST-SLF fibre crossing which enables better performance for some motor imagery and BCI participants—and is consistent with the idea of enhanced communication/synchronization between regions functionally important for this task. The causes of inter-individual variability in brain structure are not fully understood, but likely include pre-existing genetic contributions and contributions from learning and the environment [23]. Ullén et al. [26] attempted to address this by investigating whether millisecond variability in a simple, automatic timing task, isochronous finger tapping, correlates with intellectual performance and, using voxel-based morphometry, whether these two tasks share neuroanatomical substrates. Volumes of overlapping right prefrontal white matter regions were found to be correlated with both stability of tapping and intelligence. These results suggest a bottom-up explanation where extensive prefrontal connectivity underlies individual differences in both variables as opposed to top-down mechanisms such as attentional control and cognitive strategies.

Sensorimotor rhythms modulation is the most popular BCI control strategy yet little is known about the structural and functional differences which separate motor

areas related to motor output from higher order motor control areas or about the functional neural correlates of high order control areas during voluntary motor control. EEG and fMRI studies have shown the extent of motor regions which are active along with the temporal sequence of activations across different motor areas during a motor task and across different subjects [27][28]. Ball et al. [27] showed that all subjects in an EEG/fMRI study involving finger flexion had highly activated primary motor cortex areas along with activation of the frontal medial wall motor areas. They also showed that some subjects had anterior type activations as opposed to posterior activation for others, with some showing activity starting in the anterior Cingulate Motor Area (CMA) and then shifting to the intermediate supplementary motor areas. The time sequence of these activations was noted where it was shown that approximately 120ms before movement onset there was a drop in source strength in conjunction with an immediate increase of source strength in the M1 area. Those who showed more posterior activations were restricted to the posterior supplementary motor area (SMA). Some subjects show activation of the inferior parietal lobe (IPL) during early movement onset. In all subjects showing activation of higher order motor areas (anterior CMA, intermediate SMA, IPL), these areas became active before the executive motor areas (M1 and posterior SMA). A number of these areas are related to attentional processing, others for triggering and others for executing. Understanding the sequence of these events for each individual in the context of rehabilitation and more advanced brain and neural computer interfacing will be important.

The neural mechanisms of brain-computer interface control have been investigated by [28] in an fMRI study. It was shown that up to 30 different motor sites are significantly activated during motor execution, motor observation and motor imagery and that the number of activated voxels during motor observation was significantly correlated with accuracy in an EEG sensorimotor rhythm (SMR) based BCI task (see section 13.7.1 for further details on SMR). Significantly higher activations of the supplementary motor areas for motor imagery and motor observation tasks were observed for high aptitude BCI users (see Figure 13.5 for an illustration [28]). The results demonstrate that acquisition of the sensorimotor program reflected in SMR-BCI-control (section 13.7.1) is tightly related to the recall of such sensorimotor programs during observation of movements and unrelated to the actual execution of these movement sequences.

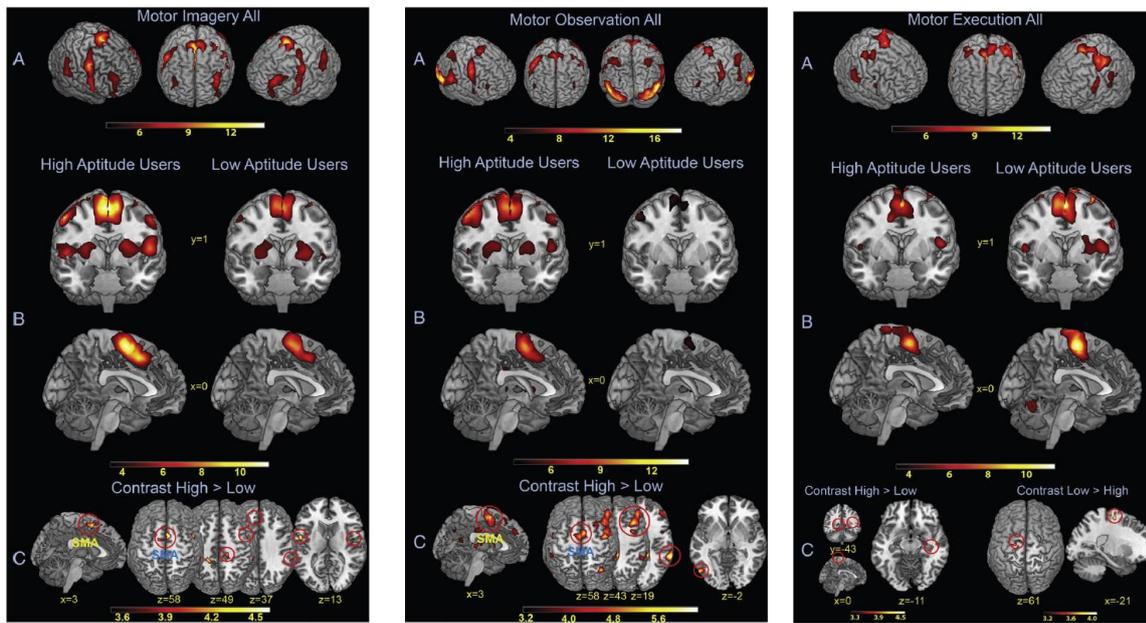


Figure 13.5 Brain activations motor imagery, motor observation task and motor execution task showing mean activation of all participants (A), high aptitude users and low aptitude users individually (B) and the contrast of high aptitude users low aptitude users (C). The figure illustrates the maximum contrast between low aptitude and high aptitude BCI users (Figure reproduced from [28] with permission from Sebastien Halder).

Using such knowledge about sensorimotor control will be critical in understanding and developing successful learning and control models for robotic devices and BCIs and fully closing the sensorimotor learning loop to enable finer manipulation abilities using BCIs and for retraining or enabling better relearning of motor actions after cortical damage. Understanding the neuroanatomy involved in motor execution/imagery/observation may also provide a means of enhancing our knowledge of motion primitives and their neural correlates as discussed in section 13.4. MRI and fMRI however only provide part of the picture, at the level of large networks of neurons, and on relatively large time scales. Invasive electrophysiological however can target specific neuronal networks at millisecond time resolution. The following section highlights some of the most recent findings from motor cortical surface potentials investigations.

13.6 Electrocorticographic Motor Cortical Surface Potentials

The electroencephalogram (EEG) is derived from the action potentials of millions of neurons firing electrical pulses simultaneously. The human brain has more than

100,000,000,000 (10^{11}) neurons and thousands of spikes (electrical pulses) are emitted each millisecond. EEG reflects the aggregate activity of millions of individual neurons recorded with electrodes positioned in a standardized pattern on the scalp. Brainwaves are categorized into a number of different frequency bands including delta (1-4Hz), theta (5-8Hz), alpha (8-12Hz), mu (8-12Hz), beta (13-30Hz) and gamma (>30Hz). Each of these brain rhythms can be associated with various brain processes and behavioral states, however, knowledge of exactly where brainwaves are generated in the brain, and if/how they communicate information, is very limited. By studying brain rhythms and oscillations we attempt to answer these questions and have realized that brain rhythms underpin almost every aspect of information processing in the brain, including memory, attention and even our intelligence. We also observe that abnormal brain oscillations may underlie the problems experienced in diseases such as epilepsy or Alzheimer's disease and we know that certain changes in brain rhythms and oscillations are good indicators of brain pathology associated with these diseases. If we know more about the function of brainwaves we may be able to develop better diagnosis and treatments of these diseases. It may also lead to better computational tools and better bio-inspired processing tools to develop artificial cognitive systems.

Brain rhythmic activity can be recorded non-invasively from the scalp as EEG or intracranially from the surface of the cortex as cortical EEG or the electrocorticogram (EEG is described in section 13.7).

Electrocorticography (ECoG), involving the clinical placement of electrode arrays on the brain surface (usually above the Dura) enable the recording of, similar to EEG, large scale field potentials that are primarily derived from the aggregate synaptic potential from large neuronal populations whereby synaptic current produces a change in the local electric field. ECoG can characterise local cortical potentials with high spatiotemporal precision (0.5cm^2 in ECoG compared to 1cm^2 in EEG) and high amplitudes (10-200 μV in ECoG compared to 10-100 μV in EEG). Furthermore, the ECoG spectral content can reach 300Hz (compared to 60Hz in EEG) due to closer vicinity of the electrodes to the electric source (the non-homogenous, anisotropic brain volume and tissues act as a low pass filter). Independent individual finger movement dynamics can be resolved at the 20-ms time scale which has been shown not possible with EEG (but has recently been demonstrated using MEG [29] as described in section 13.7). Here we review some of

the latest findings of electrocorticography studies involving human sensorimotor systems.

The power spectral density (PSD) of the cortical potential can reveal properties within neuronal populations. Peaks in the PSD indicate activity that is synchronized across a neuronal population, for example, movement decreases the lateral frontoparietal alpha (8-12Hz) and beta rhythm (12-30Hz) amplitudes with limited spatial specificity whereas high gamma changes, which are spatially more focused, are also observable during motor control. Miller et al. [30] however, observed through a range of studies investigating local gamma band-specific cortical processing, a lack of distinct peaks in the cortical potential PSD beyond 60Hz and hypothesised the existence of broadband changes across all frequencies which were obscured at low frequencies by covariate fluctuations in θ (4-7Hz), α (8-12Hz) and β (13-30Hz) band oscillations. They demonstrate that there is a phenomenon which obeys a broadband, power-law form extending across the entire frequency range. Even with local brain activity in the gamma band there is an increase in power across all frequencies and the power law shape is conserved. This suggests that there is phenomena with no special timescale where the neuronal population beneath is not oscillating synchronously but may simply reflect a change in the population mean firing rate. Miller et al. [30] postulate that the power law scaling during high γ activity is a reflection of changes in asynchronous activity and not necessarily synchronous, rhythmic, action potential activity changes as is often hypothesized.

These findings suggest a fundamentally different approach to the way we consider the cortical potential spectrum: power law scaling reflects asynchronous, averaged, input to the local neural population whereas changes in characteristic brain rhythms reflect synchronized populations that coherently oscillate across large cortical regions. Miller et al. [30] also augment the findings by demonstrating power law scaling in simulated cortical potentials using small scale, simplified integrate and fire neuronal models, an example of which is shown in Fig. 13.6.

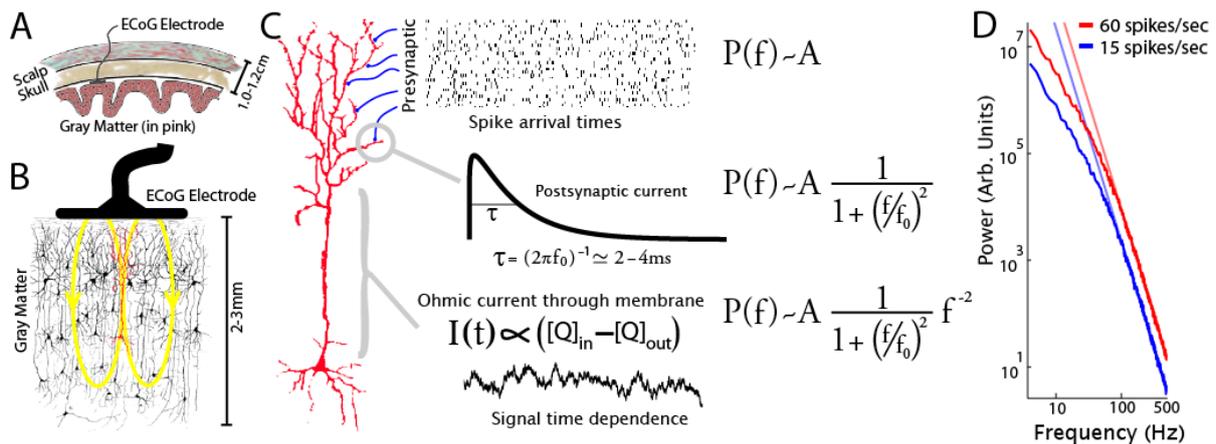


Figure 13.6 An illustration of how the power-law phenomena in the cortical potential might be generated based on a simulation study (see [30] for details). Figure (D) shows the power spectral density (PSD) of this signal and has a knee 70Hz, with a power law of $P \sim \frac{1}{f^4}$ that would normally be observed in ECoG PSD. The change in the spectra with increasing mean spike rate of synaptic input strongly resembles the change observed experimentally over motor cortex during activity as demonstrated in [30] (Figure reproduced from [30] with permission from Kai J Miller : doi:10.1371/journal.pcbi.1000609.g005).

Knowledge of this power law scaling in brain surface electric potential has been subsequently exploited in a number of further studies investigating differences in motor cortical processing during imagined and executed movements [31] and the role of rhythms and oscillations in sensorimotor activations [32].

As outlined, motor imagery to produce volitional neural signals to control external devices and for rehabilitation is one of the most popular approaches employed in brain-computer interfaces. As highlighted in the previous section neuroimaging using hemodynamic markers (PET and fMRI) and extra cerebral magnetic and electric field studies (MEG and EEG) have shown that motor imagery activates many of the same neocortical areas as those involved in planning and execution of movements. Miller et al. [31] have studied the execution-imagery similarities with electrocorticographic cortical surface potentials in eight human subjects during overt action and kinaesthetic imagery of the same movement to determine what and where are the neuronal substrates that underlie motor imagery-based learning and the congruence of cortical electrophysiologic change associated with motor movement and motor imagery. The results show that the spatial distribution of activation is significantly overlapping between hand and tongue movement in the lower frequency bands (LFB) but not in the higher frequency bands (HFB) whereas during kinaesthetic

imagination of the same movement task the magnitude of spectral changes were smaller (26% less calculated across the electrode array) even though the spatially broad decrease in power in the LFB and the focal increase in HFB power were similar for movement and imagery.

During an imagery based learning task involving real-time feedback of the magnitude of cortical activation of a particular electrode, in the form of cursor movement on screen, the spatial distribution of HFB activity was quantitatively conserved in each case, but the magnitude of the imagery associated spectral change increased significantly and, in many cases, exceeded that observed during actual movement. The spatially broad desynchronisation in LFB is consistent with EEG-based imagery which use α/β desynchronisation as a means of cursor control in BCIs [18]; however, the results demonstrate this phenomena reflects an aspect of cortical processing that is fundamentally non-specific. LFB desynchronization may reflect altered feedback between cortical and subcortical structure with a timescale of interaction that corresponds to the peak frequency in the PSD as opposed to local, somatotopically distinct, population scale computation. Miller et al. [31] speculate that the significant LFB power difference during movement and imagery might be a correlate of a partial release of cortex by subcortical structures (partial decoherence of a synchronised corticothalamic circuit) as opposed to a complete release during actual movement or after motor imagery feedback.

The HFB change is reflective of a broadband PSD increase that is obscured at lower frequencies by the motor associated α/β rhythms but which has been specifically correlated with local population firing rate and is observed in a number of spatially overlapping areas including primary motor cortical areas for both movement and imagery. These findings have been used to speculate a lot about the neural substrates and electrophysiology of movement control. The results clearly demonstrate the congruence in large scale activation between motor imagery and overt movement, and imagery-based feedback and the overlapping activation in distributed circuits during movement and imagery, the clear role of the primary motor cortex during motor imagery and the role of feedback in the augmentation of widespread neuronal activity during motor imagery. Electrographic evidence of the relevance of the role of primary motor areas during motor imagery to complement EEG and neuroimaging showing primary motor activation during imagery/movement such as those outlined in the previous section was also an

outcome of the study. The dramatic augmentation given by feedback, particularly in primary motor cortex is significant, particularly in the context of BCI training, because it demonstrates a dynamic restructuring of neuronal dynamics across a whole population in motor cortex on very short time scales (<10min) [31]. This augmentation and restructuring can indeed result in improved motor imager performance over time but leads to necessity to co-adapt the BCI signal processing to cope with associated non-stationary drifts in the resulting oscillations of cortical potentials (a topic which is returned to in section 13.9).

Human motor behaviours such as reaching, reading and speaking are executed and controlled by somatomotor regions of the cerebral cortex, which are located immediately anterior and posterior to the central sulcus [32]. Electrical oscillations in the lower beta band (12-20Hz) have been shown to have an inverse relationship to motor production and imagery, decreasing during movement initiation and production and rebounding (synchronization) following movement cessation and during imagery continuation in peri-central somatomotor and somatosensory cortex.

Investigations have been conducted to determine whether beta rhythms play an active role in the computations taking place in somatomotor cortex or whether it is epiphenomenon of cortical state changes influenced by the other cortical or subcortical processes [32]. There is strong correlation between the firing time of individual neurons in the primary motor cortex and the phase of the beta rhythms in the local field potential [35]. Miller et al. [32] have acquired ECoG evidence of the role of beta rhythms in the organisation of somatomotor function by analysing the broadband spectral power on fast time scales (tens of milliseconds) during rest (visual fixation) and finger flexion. The results show that cortical activity has a robust entrainment on the phase of the beta rhythms which is predominant in peri-central motor areas whereby broadband spectral changes vary with the phase of underlying motor beta rhythm. This relationship between beta rhythms and local neuronal activity is a property of the 'idling' brain (present during resting and selectively diminished during movement). Specifically, Miller et al. [32] propose that the predominant pattern for the beta range shows a tendency for brain activity, as measured by broadband power, to increase just prior to the surface negative phase and decrease just prior to the surface positive phase of the beta rhythm, which they refer to as rhythmic entrainment. The predominant phase couplings for $\theta/\alpha/\beta$ ranges are found to be different and have different spatial localisations.

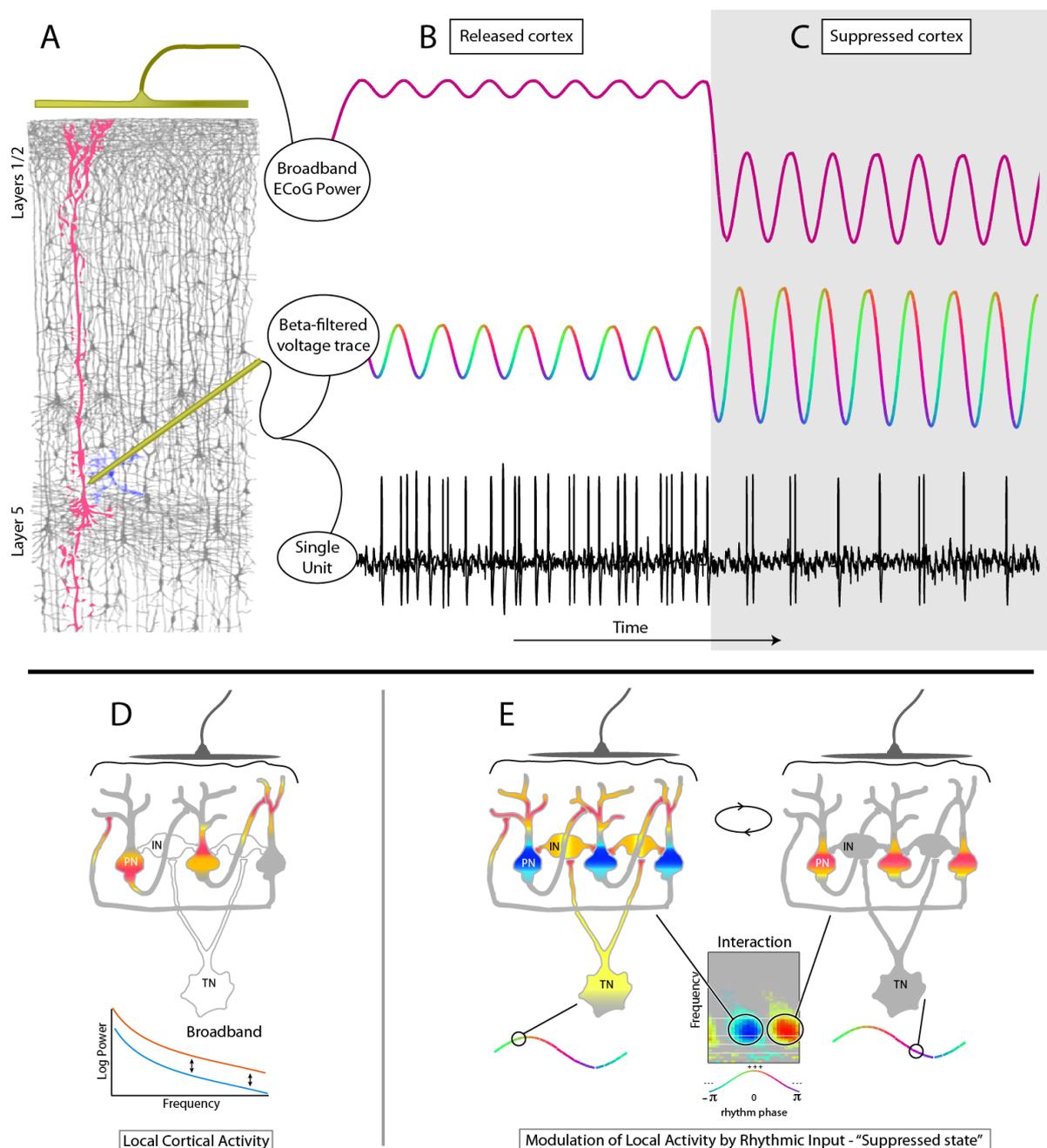


Figure 13.7 An illustration of modes of neural activity with cortical beta rhythm states. The modulation of local activity with rhythms is revealed in the ECoG by significant broadband modulation with the phase of low frequency rhythms (see [32] for further details) (Figure reproduced from [32] with permission from Kai J Miller: doi:10.1371/journal.pcbi.1000609.g005).

Miller et al. [32] proposed a 'suppression through synchronisation hypothesis', whereby diffuse cortical inputs originating from subcortical areas might functionally suppress large regions of the cortex, the advantage of which is to enable selective

engagement of task-relevant and task-irrelevant brain circuits and for dynamical reallocation of metabolic resources. This shifting entrainment suggests that the β -rhythm is not simply a background process that is suppressed during movement, but rather that the beta-rhythm plays an active and important role in motor processing. In recent years, there has been a growing focus on coupling between neuronal firing and rhythmic brain activity and this study provides substantial evidence and methodology to support the important role of brain rhythms in neuronal functioning.

13.7 MEG and EEG - Extra Cerebral Magnetic and Electric Fields of the Motor System

The previous section highlighted a number of the most recent examples of ECoG based studies that are shedding more light on the way in which the motor system processes information and is activated during imagery and movement. As Electrooculography is a highly invasive procedure involving surgery, a key question been addressed is whether the spectral findings and spatial specificity of ECoG will ever be possible using non-invasive extracerebrally acquired EEG, or whether ECoG findings can be used to develop better EEG based processing methodologies to extract ECoG information. At the International BCI meeting in 2010 a workshop addressed the critical questions around state of the art BCI signal processing, in particular, *should future BCI research emphasise a shift from scalp-recorded EEG to ECoG, and how are the signals from the two modalities related?* [36].

There is still a lot of debate around the future of EEG for BCI due to its limited spatial resolution and various noise related issues, whereas ECoG shows a lot of promise in addressing both of these issues. However, ECoG requires surgical implantation and the long-term effectiveness remains to be verified in humans. A step toward answering this question is to better understand the relationship between EEG and ECoG. In a workshop summary the question was addressed by comparing and contrasting the contribution of population synchronized (rhythmic) and asynchronous changes in the EEG and ECoG potential measurements [36]. Beta rhythm is robust in extracerebral EEG recordings, spatially synchronous across the pre and post central gyri, so this coherent rhythm is augmented with respect to background spatial averaging. The different states of the surface rhythms may represent switching between stable modes observed in on-going surface oscillations.

In contrast, the broadband spectral change that accompanies movement is asynchronous at the local level and unrelated across cortical regions so it is distorted or diminished by spatial averaging. Krusienski et al. [36] compared the contribution of population synchronized (rhythmic) and asynchronous (broadband, $1/f$) changes in the EEG and ECoG potential measurements using a number of simplifications and approximations. These approximations suggest that synchronized cortical oscillations may be differently reflected at the EEG scale than the ECoG scale. Krusienski et al. [36] show that to have the same contribution to EEG that a single cortical column has on ECoG, the spatial extent of cortical activity would have to span nearly the full width of a gyrus, and nearly a centimeter longitudinally. Based upon ECoG measurements of the $1/f$ change in the visual cortex, the findings confirm the possibility of detecting $1/f$ change in EEG during visual input directly over the occipital pole as an event related potential. In the Precentral motor cortex, the movement of several digits in concert can produce a widespread change, dramatic enough to be measured in the EEG however, based on these findings, the detection of single finger digit movement in EEG is not possible. This finding has been supported in other recent studies, a number of which involved magnetoencephalography (MEG). As with EEG, the magnetoencephalogram (MEG) is recorded non-invasively, however MEG is a record of magnetic fields, measured outside the head, produced by electrical activity within the brain whereas EEG is a measure of the electrical potentials. Synchronized neuronal currents, produced primarily by the intracellular electrical currents within the dendrites of pyramidal cells in the cortex, induce weak magnetic fields. Neuronal networks of 50,000 or more active neurons are needed to produce a detectable signal using MEG. MEG has number of advantages over EEG, most notably its spatial specificity as the magnetic flux detected at the surface of the head with MEG penetrates the skull and tissues without significant distortion, unlike the secondary volume currents detected outside the head with EEG [37]. MEG, however, is also less practical, requiring significant shielding from environmental electric magnetic interference and is not a wearable or mobile technology like EEG and therefore cannot be used for large bedside recordings in a clinical setting or mobile BCI applications. MEG has been used in a range of clinical applications (cf. [37] for a review) and for research. Below we describe a number of studies with focus on motor cortical investigations in the context of developing brain-computer interfaces.

Quandt et al. [29] have investigated single trial brain activity in non-invasive MEG and EEG recordings elicited by finger movement on one hand. The muscle mass involved in finger movement is smaller than in limb or hand movement and neuronal discharges of motor cortex neurons are correspondingly smaller in finger movement than in arm or wrist movements. This makes detection of finger movement more difficult from non-invasive recordings. Kauhanen et al. [38][39] showed using MEG that left and right hand index finger movement could be discriminated and that single trial brain activity recorded non-invasively could be used to decode finger movement; however, there is significant obstacles in non-invasive recordings in terms of the substantial overlapping activations in M1 when decoding individual fingers movement on the same hand. Miller et al. [40] and Wang et al. [41] have shown real time representation of individual finger movements is possible using ECoG; however, finger movement discrimination from extracerebral neural recordings has only recently been shown to be possible. Quandt et al. [29] found using simultaneously recorded EEG and MEG that finger discrimination on the same hand is possible with MEG but EEG is not sufficient for robust classification. The lower spatial resolution of scalp signal EEG is due to the spatial blurring at the interface of tissues with different conductance. The issue cannot be overcome by increasing the density of EEG electrodes. It is speculated that the strong curvature of the cortical sheet in the finger knob (an omega shaped knob of the central sulcus) contributes to high decoding accuracy of MEG whereby orientation change in the active tissue could change spatial patterns of magnetic flux measured in sensor space but potentials caused by the same processes are not detectable at the scalp. Using different approaches four fingers on the same hand could be decoded with circa 57% accuracy using MEG and across all cases MEG performs better than EEG ($p < 0.005$) whilst EEG often only produced accuracies slightly above the upper confidence interval for guessing.

Analysis of the oscillations from MEG correspond to ECoG studies where the power of the lower oscillations (<60Hz) decrease around the movement, whereas power in the high gamma band increases and that the effects in the high gamma band are more spatially focused than in the lower frequency bands [29]. Interestingly, the discrimination accuracy from band power of the most informative frequency band between 6Hz and 11Hz was clearly inferior to accuracy derived from the time series data, indicating that slow movement related neural activation modulations are most informative about which finger of a hand moves and the

inferior accuracy given by band power is likely due to lack of phase information contained in band power features [29] (time embedding, temporal sequence information and exploiting phase information in discriminating motor signals are revisited in section 13.9).

The above are just a few examples of what has shown not to be possible to characterise sufficiently in EEG. The following subsection provides an overview of the known sensorimotor phenomena detectable from EEG and some of the most recent advances in decoding hand/arm movements noninvasively.

13.7.1 Sensorimotor Rhythms and Other Surrounding Oscillations

There are a number of rhythms and potentials that have been strongly linked with motor control, many of which have been exploited in EEG based non-invasive BCI devices. As outlined previously, the sensorimotor area (SMA) generates a variety of rhythms that have specific functional and topographic properties. To reiterate, distinct rhythms are generated by hand movements over the post central somatosensory cortex. The μ (8-12Hz) and β (13-30Hz) bands are altered during sensorimotor processing [33][34][42]. Attenuation of the spectral power in these bands indicates an event related desynchronization (ERD) whilst an increase in power indicates event-related synchronization (ERS). ERD of the μ and β bands are commonly associated with activated sensorimotor areas and ERS in the mu band is associated with idle or resting sensorimotor areas. ERD/ERS has been studied widely for many cognitive studies and provides very distinctive lateralized EEG pattern differences which form the basis of left vs. right hand or foot MI-based BCIs [43][44]. However, as outlined above, later studies have shown the actual rhythmic activity generated by the sensorimotor system can be much more detailed. The α or μ component of the SMR also has a phase coupled second peak in the beta band. Both the alpha and beta peak can become independent at the offset of a movement after which the beta band rebounds faster and with higher amplitude than the alpha band. Desynchronization of the beta band during a motor task can occur in different frequency bands than the subsequent resynchronization (rebound) after the motor task [33]. As previously outlined many studies have shown that neural networks similar to those of executed movement are activated during imagery and observation of movement and thus similar sensorimotor rhythmic activity can be observed during motor imagery and execution.

Gamma oscillations of the electromagnetic field of the brain are known to be involved in a variety of cognitive processes and are believed to be fundamental for information processing within the brain. Gamma oscillations have been shown to be correlated with other brain rhythms at different frequencies and a recent study has shown the causal influences of gamma oscillation on sensorimotor rhythms (SMR) in healthy subjects using magnetoencephalography [45]. It has been shown that the modulation of sensorimotor rhythms is positively correlated with the power of frontal and occipital gamma oscillations, negatively correlated with the power of centro-parietal gamma oscillations and that simple causal structure can be attributed to a causal relationship or influence of gamma oscillations on the SMR. The behavioural correlate of the topographic alterations of gamma power, a shift of gamma power from centro-parietal to frontal and occipital regions, remains elusive although increased gamma power over frontal areas has been associated with selective attention in auditory paradigms. Grosse-Wentrup et al. [45] postulate that neurofeedback of gamma activity may be used to enhance BCI performance to help low aptitude BCI users i.e., those who appear incapable of BCI control using SMR.

13.7.2 Movement Related Potentials

Signals observed during and before the onset of movement signify motor planning and preparation. For example, the Bereitschafts Potential or BP (from German, "readiness potential"), also called the pre-motor potential or readiness potential (RP), is a measure of activity in the motor cortex of the brain leading up to voluntary muscle movement [46][47]. The BP is a manifestation of cortical contribution to the pre-motor planning of volitional movement. Krauledat et al. [48][49] report on experiments carried out using the lateralised readiness potential (LRP) (i.e., Bereitschafts Potential) for brain-computer interfaces. Before accomplishing motor tasks a negative readiness potential which reflects the preparation can be observed. They showed it was possible to distinguish the pre-movement potentials from finger tapping experiments, even before the movement occurs or the onset of the movement thus potentially improving accuracy and reducing latency in the BCI system. The BP is ten to hundred times smaller than the α -rhythm of the EEG and it can only be identified by averaging across trials and has two components: an early component referred to as BP1 (sometime NS1) lasting from about -1.2 to -0.5 second before movement onset (Negative Slope of early BP)

and a late component (BP2 or NS2) from -0.5 to shortly before 0 sec (steeper Negative Slope of late BP) [47][50][51]. A pre-movement positivity can be observed along with a motor-potential which starts about fifty to sixty milliseconds before the onset of movement and has its maximum over the contralateral Precentral hand area.

13.7.3 Decoding Hand Movements from EEG

Movement-related cortical potentials (MRCP) have been used as control signals for BCIs [52]. MRCP and SMR have distinct changes during execution or imagination of voluntary movements. MRCP is considered a slow cortical potential where the surface negativity which develops two seconds before the movement onset is the Bereitschaftspotential referred to above. Gu et al. [52] studied MRCP and SMRs in the context of discriminating the movement type and speed from the same limb based on the hypothesis that if the imagined movements are related to the same limb, the control could be more natural than associating commands to movements of different limbs for BCIs. They focused on fast slow wrist rotation and extension and they found that average MRCPs rebounded stronger when fast-speed movements were imagined compared with slow-speed movements; however, the rebound rate of MRCP was not substantially different between movement types. The peak negativity was more pronounced in the frontal (Fz) and central region (C1) than in the occipital region (Pz). The rebound rate of MRCP was greater in the central region (C1) when compared to the occipital region (Pz). MRCP and SMR are independent of each other as they originate from different brain sources and they occupy different frequency bands [51][52][53]. This renders them useful for multidimensional control in BCIs.

In accordance with the analysis of averaged MRCPs, the single-trial classification rate between two movements performed at the same speed was lower than when combining movements at different speeds. Gu et al. [52] suggest that selecting different speeds rather than different movements when these are executed at the same joint may be best for BCI applications. However, the task pair which was optimal in terms of classification accuracy is subject dependent thus a subject-specific evaluation of the task pair should be conducted. This study by Gu et al. [52] is important as it is one of a limited number of studies that focus on discriminating different movements of the same limb as opposed to moving different limbs from

EEG, which is much more common practice in BCI designs. However, Lakany & Conway [54] investigated the difference between imagined and executed wrist movements in 20 different directions using machine learning and found that the accuracy of discriminating wrist movement imagination is much less than for actual movement; however, they later found [55] time-frequency EEG features modulated by force direction in arm isometric exertions to four different directions in the horizontal plane can give better directional discrimination information and that t-f features from the planning and execution phase may be most appropriate.

Although a limited number of EEG-based 2D and 3D continuous control of a cursor through biofeedback training using BCI have been reported [56][57] along with a few studies of classification of the direction/speed of 2D hand/wrist movements outlined above, there are very few studies that have demonstrated continuous decoding of hand kinematics from EEG. Classification of different motor imagery tasks on single trial basis is more commonly reported. The signal-to-noise ratio, the bandwidth, and the information content of electroencephalography are generally thought to be insufficient to extract detailed information about natural, multi-joint movements of the upperlimb. However, evidence from a study by Bradberry et al. [58] investigating if the kinematics of natural hand movements are decodable from EEG challenges this assumption. They continuously extract hand velocity from signals collected during a three-dimensional (3D) center-out reaching task and found that that a linear EEG decoding model could reconstruct 3D hand-velocity profiles reasonably well and that sensor CP3 which lies roughly above the primary sensorimotor cortex contralateral to the reaching hand made the greatest contribution. Using a time lagged approach they found that EEG data from 60ms in the past supplied the most information with 16.0% of the total contribution suggesting linear decoding method such as the one used [58] rely on a subsecond history of neural data to reconstruct hand kinematics. Using a source localisation technique they found that the primary sensorimotor cortex (Precentral gyrus and Postcentral gyrus) was indeed a major contributor along with the inferior parietal lobule (IPL) all of which have been found to be activated during motor execution and imagery in other investigations [11][12][15]. Bradberry et al. [58] also found the movement variability is negatively correlated with decoding accuracy suggesting two reasons; 1. increased movement variability could degrade decoding accuracy due to less similar pairs of EEG–kinematic exemplars i.e., less movement variability results in reduced

intra-class variability for training and 2. subjects differ in their ability to perform the task without practice (motor learning is important for improving predictions of movement); hence, the strengths of a priori neural representations of the required movements vary until learned or practiced and these differences could directly relate to the accuracy with which the representations can be extracted. This study provides important evidence that decodable information about detailed, complex hand movements can be derived from the brain non-invasively using EEG however it remains to be determined if these findings are consistent when using the same methodology in an imagined 3D center-out task.

Although we know a lot about brain structure associated with sensorimotor activity as well as the rhythms and potentials surrounding this activity we have not yet systematically linked the neural correlates of these to specific motion primitives or motor control models. Modelling, using biological plausible neural models, the findings in relation to motor cortical structure, function and dynamics along with linkage to the underlying motor psychophysics and advanced signal processing in BCI may help advance our knowledge on motion primitives, sensorimotor learning and control.

13.8 Extracellular Recording - Decoding Hand Movements from Spikes and Local Field Potential

Although fMRI, MEG and EEG offer the low risk non-surgical recording procedure they have inherent limitations which many expect can be overcome with invasive approaches such as ECoG (described in section 13.6) and by implanting electrodes to record the electrical activity of single neurons extracellularly (single unit recordings). Here we focus on some recent studies aimed at testing this scale for use in sensorimotor related BCIs.

Extracellular recording has many advantages including high signal amplitude (up to $500\mu\text{V}$), low susceptibility to external noise and artefact (eye movements, cardiac activity, muscle activity) leading to high signal-to-noise ratio, high spatial resolution ($50\mu\text{m}^2$), high temporal resolution ($\sim 1\text{msec}$) and high spectral content (up to 2KHz) due to the close vicinity to the electric source. As a consequence, there is a high correlation between the neural signals recorded and the generated / imagined hand movements resulting in a short learning duration when employed in a motor BCI system. The disadvantages of the invasive recording technique include a

complex and expensive medical procedure, susceptibility to infections (possibly leading to meningitis, epilepsy), pain, prolonged hospitalization, direct damage to the neural tissue (e.g., a flat $15\mu\text{m} \times 60\mu\text{m}$ electrode penetrating 2mm deep hits, on average, 5 neurons and 40,000 synapses), indirect damage to the neural tissue (small blood vessels are hit by the electrode causing ischemia for distant neurons and synapses and the evolution of an inflammatory response) and evolvment of a scarred tissue which electrically isolates the electrodes from the surroundings and render the system non-responsive after being implanted for extended durations. Furthermore, the electrode material itself, however biocompatible, causes sooner or later an inflammatory reaction and the evolvment of a scarred tissue.

Theoretically, however extracellular recordings offer more accurate information that may enable devise realistic BCI systems that allow for additional degrees of freedom and natural control of prosthetic devices, such as a hand and arm prostheses. To this end, substantial efforts have been put into devising novel biocompatible electrodes (e.g., Platinum, Iridium Oxide, carbonic polymers) that will delay immune system stimulation, devising multi-functional microelectrodes which allow for recording / stimulating while injecting anti-inflammatory agents to suppress inflammatory response, devising hybrid microelectrodes that allow for the inclusion of preamplifier and multiplexer on the electrode chip to allow wireless transmission of the data thus avoiding the necessity for the scalp drill hole used for taking out the flat cable carrying the neural data, which is prone to infections.

Extracellular recording, being the most invasive recording technique (compared to non-invasive EEG and MEG recording and partially invasive ECoG recording) allows recording both the high frequency content neural *output* activity, .i.e., spikes, and the low frequency content neural *input* activity, denoted as Local Field Potential (LFP), which is the voltage caused by electrical current flowing from all nearby dendritic synaptic activity across the resistance of the local extracellular space. In the following section, the neural coding schemes, in general, and the cortical correlates of kinematic and dynamic motion attributes, in specific, will be presented along with their suggested use for current and future BCI systems.

13.8.1 Neural Coding Schemes

A sequence, or 'train', of spikes may contain information based on different coding schemes. In motor neurons, for example, the strength at which an innervated

muscle is flexed depends solely on the 'firing rate', the average number of spikes per unit time (a 'rate code'). At the other end, a complex 'temporal code' is based on the precise timing of single spikes. They may be locked to an external stimulus such as in the auditory system or be generated intrinsically by the neural circuitry. Whether neurons use rate coding or temporal coding is a topic of intense debate within the neuroscience community, even though there is no clear definition of what these terms mean. Neural schemes include rate coding, spike count rate, time dependent firing rate, temporal coding and population coding:

Rate coding - rate coding is a traditional coding scheme, assuming that most, if not all, information about the stimulus is contained in the firing rate of the neuron. The concept of firing rates has been successfully applied during the last 80 years. It dates back to the pioneering work of ED Adrian who showed that the firing rate of stretch receptor neurons in the muscles is related to the force applied to the muscle [59]. In the following decades, measurement of firing rates became a standard tool for describing the properties of all types of sensory or cortical neurons, partly due to the relative ease of measuring rates experimentally.

Because the sequence of action potentials generated by a given stimulus varies from trial to trial, neuronal responses are typically treated statistically or probabilistically. They may be characterized by firing rates, rather than as specific spike sequences. In most sensory systems, the firing rate increases, generally non-linearly, with increasing stimulus intensity. Any information possibly encoded in the temporal structure of the spike train is ignored. Consequently, rate coding is inefficient but highly robust with respect to the inter-spike interval (ISI) 'noise'. During recent years, more and more experimental evidences have suggested that a straightforward firing rate concept based on temporal averaging may be too simplistic to describe brain activity [60]. In rate coding, learning is based on activity-dependent synaptic weight modifications.

Spike-count rate - the spike-count rate, also referred to as temporal average, is obtained by counting the number of spikes that appear during a trial and dividing by the duration of trial. The length T of the time window is set by the experimenter and depends on the type of neuron recorded from and the stimulus. In practice, to get sensible averages, several spikes should occur within the time window. Typical values are $T = 100$ ms or $T = 500$ ms, but the duration may also be longer or shorter.

The spike-count rate can be determined from a single trial, but at the expense of losing all temporal resolution about variations in neural response during the course of the trial. Temporal averaging can work well in cases where the stimulus is constant or slowly varying and does not require a fast reaction of the organism - and this is the situation usually encountered in experimental protocols. Real-world input, however, is hardly stationary, but often changing on a fast time scale. For example, even when viewing a static image, humans perform saccades, rapid changes of the direction of gaze. The image projected onto the retinal photoreceptors changes therefore every few hundred milliseconds. Despite its shortcomings, the concept of a spike-count rate code is widely used not only in experiments, but also in models of neural networks. It has led to the idea that a neuron transforms information about a single input variable (the stimulus strength) into a single continuous output variable (the firing rate).

Time-dependent firing rate - the time-dependent firing rate is defined as the average number of spikes (averaged over trials) appearing during a short interval between times t and $t+\Delta t$, divided by the duration of the interval. It works for stationary as well as for time-dependent stimuli. To experimentally measure the time-dependent firing rate, the experimenter records from a neuron while stimulating with some input sequence. The same stimulation sequence is repeated several times and the neuronal response is reported in a Peri-Stimulus-Time Histogram (PSTH). The time t is measured with respect to the start of the stimulation sequence. The Δt must be large enough (typically in the range of one or a few milliseconds) so there is a sufficient number of spikes within the interval to obtain a reliable estimate of the average. The number of occurrences of spikes $n_K(t;t+\Delta t)$ summed over all repetitions of the experiment divided by the number, K , of repetitions is a measure of the typical activity of the neuron between time t and $t+\Delta t$. A further division by the interval length Δt yields time-dependent firing rate $r(t)$ of the neuron, which is equivalent to the spike density of PSTH.

For sufficiently small Δt , $r(t)\Delta t$ is the average number of spikes occurring between times t and $t+\Delta t$ over multiple trials. If Δt is small, there will never be more than one spike within the interval between t and $t+\Delta t$ on any given trial. This means that $r(t)\Delta t$ is also the fraction of trials on which a spike occurred between those times. Equivalently, $r(t)\Delta t$ is the probability that a spike occurs during this time interval. As

an experimental procedure, the time-dependent firing rate measure is a useful method to evaluate neuronal activity, in particular in the case of time-dependent stimuli. The obvious problem with this approach is that it cannot be the coding scheme used by neurons in the brain. Neurons cannot wait for the stimuli to repeatedly present in exactly the same manner as observed before generating the response. Nevertheless, the experimental time-dependent firing rate measure makes sense, if there are large populations of independent neurons that receive the same stimulus. Instead of recording from a population of N neurons in a single run, it is experimentally easier to record from a single neuron and average over N repeated runs. Thus, the time-dependent firing rate coding relies on the implicit assumption that there are always populations of neurons.

Temporal coding - When precise spike timing or high-frequency firing-rate fluctuations are found to carry information, the neural code is often identified as a temporal code. A number of studies have found that the temporal resolution of the neural code is on a millisecond time scale, indicating that precise spike timing is a significant element in neural coding [61]. Temporal codes employ those features of the spiking activity that cannot be described by the firing rate. For example, time to first spike after the stimulus onset, characteristics based on the second and higher statistical moments of the ISI probability distribution, spike randomness, or precisely timed groups of spikes (temporal patterns) are candidates for temporal codes. As there is no absolute time reference in the nervous system, the information is carried either in terms of the relative timing of spikes in a population of neurons or with respect to an ongoing brain oscillation.

The temporal structure of a spike train or firing rate evoked by a stimulus is determined both by the dynamics of the stimulus and by the nature of the neural encoding process. Stimuli that change rapidly tend to generate precisely timed spikes and rapidly changing firing rates no matter what neural coding strategy is being used. Temporal coding refers to temporal precision in the response that does not arise solely from the dynamics of the stimulus, but that nevertheless relates to properties of the stimulus. The interplay between stimulus and encoding dynamics makes the identification of a temporal code difficult. The issue of temporal coding is distinct and independent from the issue of independent-spike coding. If each spike is independent of all the other spikes in the train, the temporal character of the neural

code is determined by the behavior of time-dependent firing rate $r(t)$. If $r(t)$ varies slowly with time, the code is typically called a rate code, and if it varies rapidly, the code is called temporal.

Population coding - population coding is a method to represent stimuli by using the joint activities of a number of neurons. In population coding, each neuron has a distribution of responses over some set of inputs, and the responses of many neurons may be combined to determine some value about the inputs.

Currently, BCI and BMI systems rely mostly on population coding. The description of one of the most famous population code – the motor population vector along with its use in current and future BCI and BMI systems is presented in section 13.8.2.

13.8.2 Single Unit Activity Correlates of Hand Motion Attributes

In 1982, Apostolos Georgopoulos and colleagues [62] found that the activity of single cells in the motor cortex of monkey, who were making arm movements in eight directions (at 45 degrees intervals) in a two-dimensional apparatus, varied in an orderly fashion with the direction of movement. Discharge was most intense with movements in a preferred direction and was reduced gradually when movements were made in directions farther and farther away from the preferred movement. This resulted in a bell-shaped directional tuning curve. These relations were observed for cell discharge during the reaction time, the movement time, and the period that preceded the earliest changes in the electromyographic (EMG) activity (approximately 80 msec before movement onset) (Electromyography (EMG) is a technique for evaluating and recording the electrical activity produced by skeletal muscles). In about 75% of the 241 directionally tuned cells, the frequency of discharge, D , was a sinusoidal function of the direction of movement, θ :

$$D = b_0 + b_1 \sin \theta + b_2 \cos \theta \quad (13.3)$$

or, in terms of the preferred direction, θ_0 :

$$D = b_0 + c_1 \cos (\theta - \theta_0) \quad (13.4)$$

where b_0 , b_1 , b_2 , and c_1 are regression coefficients. Preferred directions differed for different cells so that the tuning curves partially overlapped. The orderly variation of cell discharge with the direction of movement and the fact that cells related to only one of the eight directions of movement tested were rarely observed indicate that movements in a particular direction are not subserved by motor cortical cells

uniquely related to that movement. It was suggested, instead, that a movement trajectory in a desired direction might be generated by the cooperation of cells with overlapping tuning curves. The Orderly variation in the frequency of discharge of a motor cortical cell with the direction of movement is shown in Figure 8.

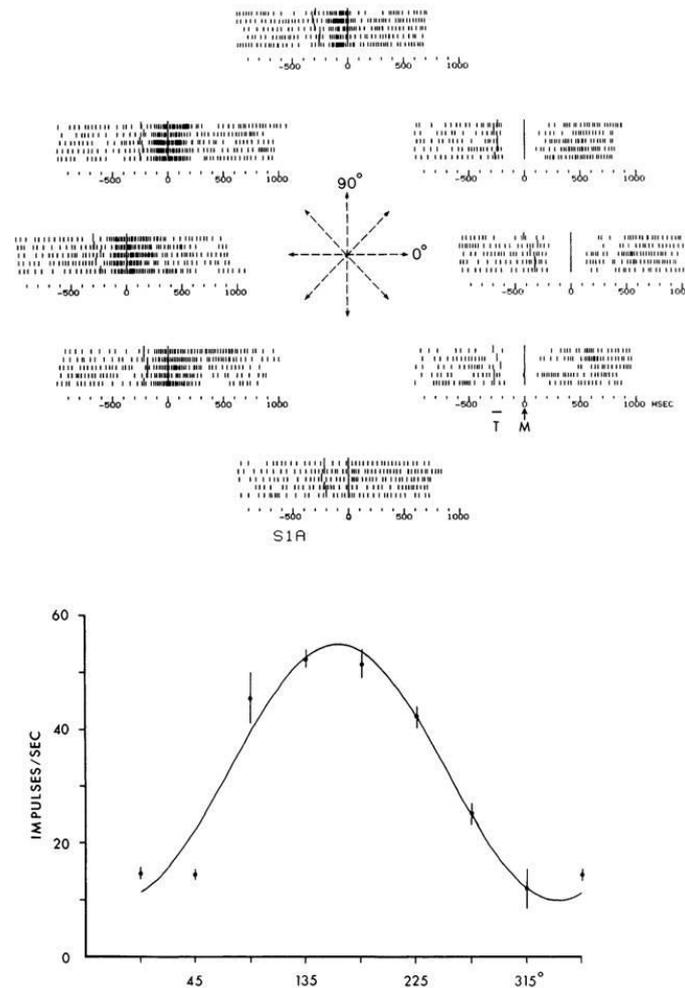


Figure 13.8 Orderly variation in the frequency of discharge of a motor cortical cell with the direction of movement. *Upper half*, Rasters are oriented to the movement onset, *M*, and show impulse activity during five repetitions of movements made in each of the eight directions indicated by the *center diagram*. Notice the orderly variation in cell's activity during the RT (reaction time), MT (movement time) and TET (total experiment time = RT+ MT). *Lower half*, Directional tuning curve of the same cell. The discharge frequency is for TET. The data points are mean \pm SEM. The regression equation for the fitted sinusoidal curve is $D = 32.37 + 7.281 \sin \Theta - 21.343 \cos \Theta$, where D is the frequency of discharge and Θ is the direction of movement, or, equivalently, $D = 32.37 + 22.5 \cos(\Theta - \Theta_0)$, where Θ_0 is the preferred direction ($\Theta_0 = 161^\circ$) (Figure reproduced from [62] with permission from Georgopoulos).

Later on, Amirikian and Georgopoulos systematically examined the variation in the shape of the directional tuning profiles among a population of cells recorded from the arm area of the motor cortex of monkeys using movements in 20 directions, every 18 degrees [63]. This allowed the investigation of tuning functions with extra parameters to capture additional features of the tuning curve (i.e. tuning breadth, symmetry, and modality) and determine an 'optimal' tuning function. It was concluded that motor cortical cells are more sharply tuned than previously thought.

Paninski et al. [64] using a pursuit-tracking task (PTT) in which a monkey had to continuously track a randomly moving visual stimulus (thus providing a broad sample of velocity and position space) with invasive recordings from M1 region showed that there is heterogeneity of position and velocity coding in that region, with markedly different temporal dynamics for each - velocity-tuned neurons were approximately sinusoidally tuned for direction, with linear speed scaling; other cells showed sinusoidal tuning for position, with linear scaling by distance. Velocity encoding led behavior by about 100 ms for most cells, whereas position tuning was more broadly distributed, with leads and lags suggestive of both feedforward and feedback coding. Linear regression methods confirmed that random, 2-D hand trajectories can be reconstructed from the firing of small ensembles of randomly selected neurons (3-19 cells) within the M1 arm area. These findings demonstrate that M1 carries information about evolving hand trajectory during visually guided pursuit tracking, including information about arm position both during and after its specification.

Georgopoulos and colleagues formulated a population vector hypothesis to explain how populations of motor cortex neurons encode movement direction [65]. In the population vector model, individual neurons 'vote' for their preferred directions using their firing rate. The final vote is calculated by vectorial summation of individual preferred directions weighted by neuronal rates. This model proved to be successful in description of motor-cortex encoding of 2D and 3D reach direction, and was also capable of predicting new effects, e.g., accurately describing mental rotations made by the monkeys that were trained to translate locations of visual stimuli into spatially shifted locations of reach targets [66][67].

The population vector study actually divided the field of motor physiologists between Evarts' "upper motor neuron" group, which followed the hypothesis that motor cortex neurons contributed to control of single muscles [68] and the Georgopoulos group studying the representation of movement directions in cortex.

From the theoretical point of view, population coding is one of a few mathematically well-formulated problems in neuroscience. It grasps the essential features of neural coding and yet, is simple enough for theoretic analysis. Experimental studies have revealed that this coding paradigm is widely used in the sensor and motor areas of the brain. For example, in the visual area medial temporal (MT) neurons are tuned to the movement direction. In response to an object moving in a particular direction, many neurons in MT fire, with a noise-corrupted and bell-shaped activity pattern across the population. The moving direction of the object is retrieved from the population activity, to be immune from the fluctuation existing in a single neuron's signal.

Population coding has a number of advantages, including reduction of uncertainty due to neuronal variability and the ability to represent a number of different stimulus attributes simultaneously. Population coding is also much faster than rate coding and can reflect changes in the stimulus conditions nearly instantaneously. Individual neurons in such a population typically have different but overlapping selectivities, so that many neurons, but not necessarily all, respond to a given stimulus. The Georgopoulos vector coding is an example of simple averaging. A more sophisticated mathematical technique for performing such a reconstruction is the method of maximum likelihood based on a multivariate distribution of the neuronal responses. These models can assume independence, second order correlations [69] or even more detailed dependencies such as higher order maximum entropy models [70]

The finding that arm movement is well represented in populations of neurons recorded from the motor cortex has resulted in a rapid advancement in extracellular recording based BCI in non-human primates and in a limited number of human studies. Several groups have been able to capture complex brain motor cortex signals by recording from neural ensembles (groups of neurons) and using these to control external devices. First, cortical activity patterns have been used in BCIs to show how cursors on computer displays can be moved in two- and three-dimensional space. It was later realized that the ability to move a cursor can be useful in its own right and that this technology could be applied to restore arm and hand function for amputees and the physically impaired.

Miguel Nicolelis has been a prominent proponent of using multiple electrodes spread over a greater area of the brain to obtain neuronal signals to drive a BCI.

Such neural ensembles are said to reduce the variability in output produced by single electrodes, which could make it difficult to operate a BCI. After conducting initial studies in rats during the 1990s, Nicolelis and his colleagues succeeded in building a BCI that reproduced owl monkey movements while the monkey operated a joystick or reached for food [71]. The BCI operated in real time and could also control a separate robot remotely over Internet protocol. But the monkeys could not see the arm moving and did not receive any feedback, a so-called open-loop BCI.

Other laboratories which have developed BCIs and algorithms that decode neuron signals include those run by John Donoghue, Andrew Schwartz and Richard Andersen. These researchers have been able to produce working BCIs, even using recorded signals from far fewer neurons than did Nicolelis (15–30 neurons versus 50–200 neurons). Donoghue's group reported training rhesus monkeys to use a BCI to track visual targets on a computer screen (closed-loop BCI) with or without assistance of a joystick [72].

Later experiments by Nicolelis using rhesus monkeys succeeded in closing the feedback loop and reproduced monkey reaching and grasping movements in a robot arm. With their deeply cleft and furrowed brains, rhesus monkeys are considered to be better models for human neurophysiology than owl monkeys. The monkeys were trained to reach and grasp objects on a computer screen by manipulating a joystick while corresponding movements by a robot arm were hidden [73][74]. The monkeys were later shown the robot directly and learned to control it by viewing its movements. The BCI used velocity predictions to control reaching movements and simultaneously predicted handgripping force.

the use of cortical signals to control a multi-jointed prosthetic device for direct real-time interaction with the physical environment ('embodiment') was first demonstrated by Andrew Schwartz et al. [75]. Schwartz et al. implanted 96 intracortical microelectrodes in the proximal arm region of the primary motor cortex of monkeys (*Macaca mulatta*) and used their motor cortical activity to control a mechanized arm replica and control a gripper on the end of the arm. The monkey could feed itself pieces of fruit and marshmallows using a robotic arm controlled by the animal's own brain signals. Owing to the physical interaction between the monkey, the robotic arm and objects in the workspace, this new task presented a higher level of difficulty than previous virtual (cursor-control) experiments.

In 2012 Schwartz et al. [67] showed that a 52-year-old individual with tetraplegia who was implanted with two 96-channel intracortical microelectrodes in the motor cortex could rapidly achieve neurological control of an anthropomorphic prosthetic limb with seven degrees of freedom (three-dimensional translation, three-dimensional orientation, one-dimensional grasping). The participant was able to move the prosthetic limb freely in the three-dimensional workspace on the second day of training. After 13 weeks, robust seven-dimensional movements were performed routinely. The participant was also able to use the prosthetic limb to do skillful and coordinated reach and grasp movements that resulted in clinically significant gains in tests of upper limb function. No adverse events were reported.

In addition to predicting kinematic and kinetic parameters of limb movements, BCIs that predict electromyographic or electrical activity of the muscles of primates are being developed [76]. Such BCIs could be used to restore mobility in paralyzed limbs by electrically stimulating muscles. Miguel Nicolelis and colleagues demonstrated that the activity of large neural ensembles can predict arm position. This work made possible creation of BCIs that read arm movement intentions and translate them into movements of artificial actuators. Carmena and colleagues [73] programmed the neural coding in a BCI that allowed a monkey to control reaching and grasping movements by a robotic arm. Lebedev and colleagues [74] argued that brain networks reorganize to create a new representation of the robotic appendage in addition to the representation of the animal's own limbs.

The biggest impediment to BCI technology at present is the lack of a sensor modality that provides safe, accurate and robust access to brain signals. It is conceivable or even likely however, that such a sensor will be developed within the next twenty years. The use of such a sensor should greatly expand the range of communication functions that can be provided using a BCI.

To conclude, this demonstration of multi-degree-of-freedom embodied prosthetic control paves the way towards the development of dexterous prosthetic devices that could ultimately achieve arm and hand function at a near-natural level.

13.8.3 Local Field Potential Correlates of Hand Motion Attributes

Local field potentials can be recorded with extracellular recordings and a number of studies have shown their application, however, as ECoG and EEG (covered in

sections 13.5 and 13.6) are an indirect measures of LFPs we do not cover LFPs here again for brevity.

13.9 Translating Brainwaves into Control Signals - BCIs

Heretofore the chapter has focused on the characteristics of the neural correlates of motor control and how these might be deployed in SMR based EEG, ECoG and MEG BCI designs, providing evidence of activations at various scales of the brain and a brief outline of individual methodologies for attaining this evidence. Brain-computer interfaces however require a number of stages of signal processing and components to be effective and robust. Figure 13.9 shows common components of a complete BCI system. Although not all components shown are deployed together in every system there is increasing evidence that combining the best approaches deployed for each component and process in a multistage framework as well as ensemble methods or multi-classifier approaches can lead to significant performance gains when discriminating sensorimotor rhythms and translating brain oscillations into stable and accurate control signals. Performance here can be considered from various perspectives including the system accuracy in producing the correct response, the speed at which a response is detected (or the number of correct detections possible in a given period), the adaptability to each individual and the inherent non-stationary dynamics of the mutual interaction between the brain and the translating algorithm, the length of training required to reach an acceptable performance, the number of sensors required to derive a useful control signal, the amount of engagement needed by the participant to name but a few. The following sections highlight some of the methods which have been tried and tested in sensorimotor rhythm BCIs however the coverage is by no means exhaustive. Also, the main emphasis is on EEG-based BCI designs as EEG-based BCI has been the driving force behind much of the novel signal processing research conducted in the field over the last 20 years, with some of the more invasive approaches considered less usable in the short term, high risk for experimentation and deployment in humans with less funding to develop invasive strategies and less data availability.

EEG being the least informative, spectrally and spatially, about the underlying brain processes and subject to deterioration and spatial diffusion by the physical properties of the cerebrospinal fluid, skull, and skin as well as the ominous susceptibility to contamination from other sources such as muscle and eye movements, poses the most challenges for engineers, mathematicians, computer

scientists. Researchers in these, among many other disciplines, are eager to solve a problem which has dogged the field for long namely, creating an EEG based BCI which is accurate and robust across time for individual subjects and can be deployed across multiple subjects easily to offer a communication channel which matches or surpasses, at least, other basic, tried and tested computer peripheral input devices and/or basic assistive communication technologies. Signal processing as Fig. 13.10 shows, is only one piece of the puzzle with a range of other components equally as important including electrode technologies and hardware being critical to data quality, usability and acceptability of the system. Additionally, the technologies and devices under the control of the BCI is another aspect not dealt with here but a topic which requires investigation to determine how applications can be adapted to cope with the, as yet, inevitable inconsistencies in the communication and control signals derived from the BCI. Here our attention is not to deal with these elements of brain computer interface but only to provide the reader with an indicative overview of key signal processing and discrimination topics under consideration in the area, perhaps not topics which have received the attention deserved, but show promise. Interested readers are referred to [77][78][79][80][81][82][83][84][85][86] for comprehensive surveys of BCI control strategies and signal processing strategies.

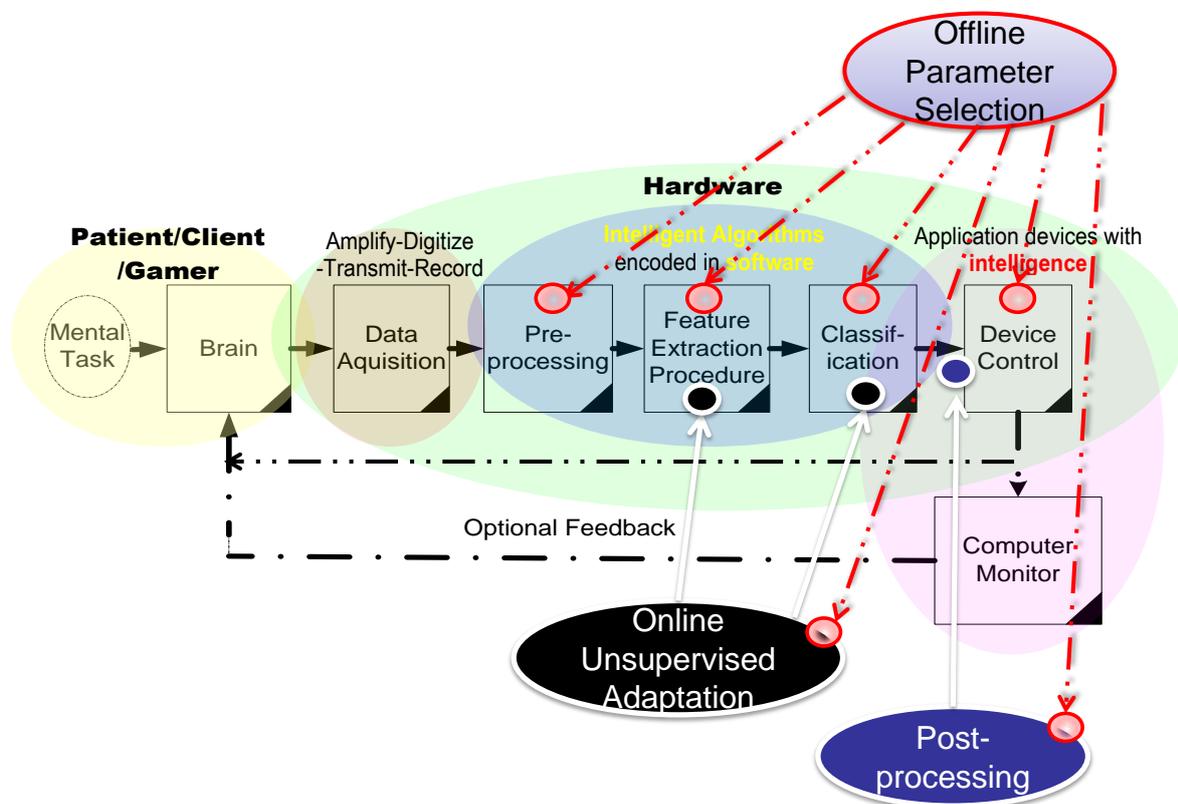


Figure13.9 An illustration of the various components of a BCI involving a closed loop learning system as well as offline and online parameter optimisation and system adaptation.

13.9.1 Preprocessing and Feature Extraction/Selection

Oscillatory and rhythmic activity in various frequency bands are a predominant feature in sensorimotor rhythm based BCIs as outlined in section 13.7.1. Whilst amplitude of power in subject-specific sub bands has proven to be a reliable feature to enable discrimination of lateralized brain activity associated with gross arm movement imagination from EEG, there is a general consensus that there is a necessity to extract much more information about spatial and temporal relationship by correlating the synchronicity, amplitude, phase and coherence of oscillatory activity across distributed brain regions. To that end, spectral filtering is often accompanied with spatial pattern estimation techniques, channel selection techniques along with other preprocessing techniques to detect signal sources and for noise removal. These include principle component analysis (PCA) and independent component analysis (ICA) among others whilst the most commonly used is the common spatial patterns (CSP) approach [87][88][89][90].

Many of these methods involve linear transformations where a set of possibly correlated observations are transformed into a set of uncorrelated variables and can be used for feature dimensionality reduction, artifact removal, channel selection and dimensionality reduction. CSP is by far the most commonly deployed of all these filters in sensorimotor rhythm based BCIs.

CSP maximizes the ratio of class-conditional variances of EEG sources [87][88]. To utilise CSP, Σ_1 and Σ_2 are the pooled estimates of the covariance matrices for two classes, as follows:

$$\Sigma_c = \frac{1}{l_c} \sum_{i=1}^{l_c} X_i X_i^t \quad (c \in \{1,2\}) \quad (13.5)$$

where l_c is the number of trials for class c and X_i is the $M \times N$ matrices containing the i^{th} windowed segment of trial i ; N is the window length and M is the number of EEG channels. The two covariance matrices, Σ_1 and Σ_2 , are simultaneously diagonalized such that the Eigenvalues sum to 1. This is achieved by calculating the generalised eigenvectors W :

$$\Sigma_1 W = (\Sigma_1 + \Sigma_2)WD \quad (13.6)$$

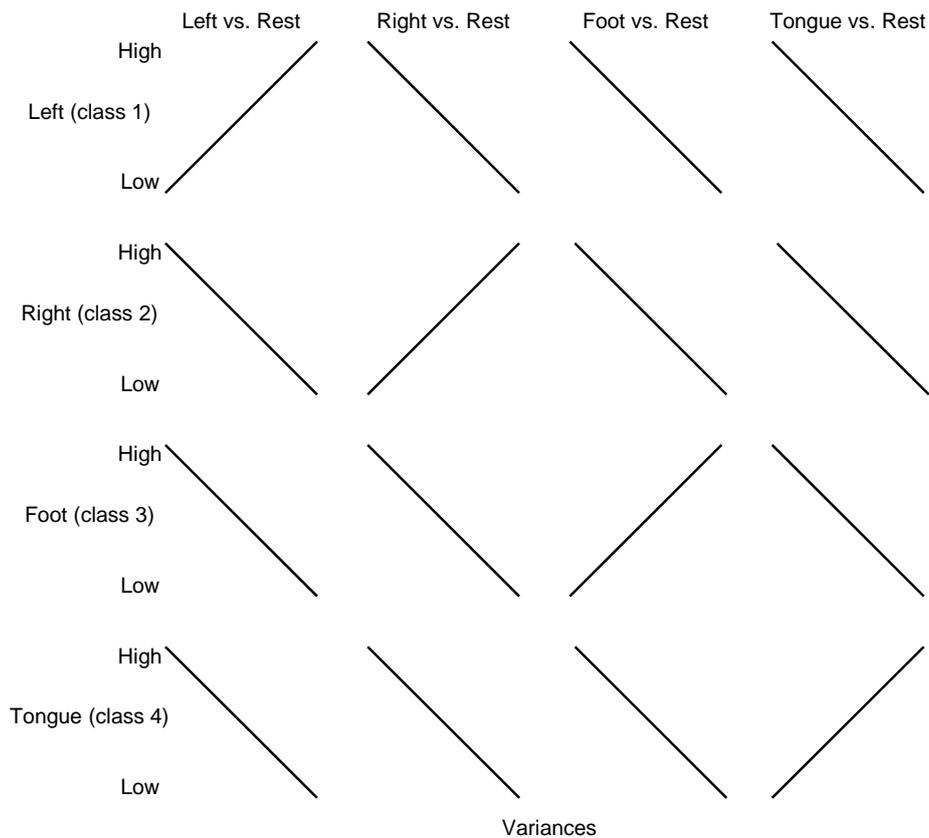


Figure 13.10 Hypothetical relative variance levels of the CSP transformed surrogate data.

where the diagonal matrix D contains the Eigenvalue of Σ_1 and the column vectors of W are the filters for the CSP projections. With this projection matrix the decomposition mapping of the windowed trials X is given as

$$E = WX. \quad (13.7)$$

To generalize CSP to three or more classes (multiclass paradigm), spatial filters can be produced for each class vs. the remaining classes (one vs. rest approach). If q is the number of filters used then there are $q \times C$ surrogate channels from which to extract features. To illustrate how CSP enhances separability among four classes the hypothetical relative variance level of the data in each of the four classes are shown in Fig. 13.10.

CSP has been modified and improved substantially using numerous techniques and deployed and tested in BCIs [87][88][89][90][91]. CSP is commonly applied with spectral filters. One of the more successful approaches to spectral filtering combined with CSP is the filter bank CSP approach [92][93]. Another promising technique for

the analysis of multi-modal, multi-channel, multitasks, multi subject and multidimensional data is multi-way (array) tensor factorization / decomposition [94]. The technique was shown to have the ability to discriminate between different conditions, such as right hand motor imagery, left hand motor imagery or both hands motor imagery, based on the spatiotemporal features of the different EEG tensor factorization components observed.

Due to the short sequences of events during motor control it is likely that assessment of activity at a fine granularity such as the optimal embedding parameters for prediction as well as the predictability of EEG over short and long time spans and across channels will also provide clues about the temporal sequences of motor planning and activations and the motion primitives involved in different hand movement trajectories. Work has shown that subject-, channel- and class-specific optimal time embedding parameter selection using partial mutual information improves the performance of a predictive framework for EEG classification in SMR-based BCIs [95][96][91][97]. Many other time series modeling, embedding and prediction through traditional and computational intelligence techniques such as fuzzy and recurrent neural networks (FNNs and RNNs) have been promoted for EEG preprocessing and feature extraction to maximize signal separability [18][65–68][102].

The above preprocessing or filtering frame works have been used extensively however rarely independently but in conjunction with a stream of other signal processing methodologies to extract reliable information from neural data. It is well known that the amplitude and the phase of neural oscillations are spatially and temporally modulated during sensorimotor processing (see section 13.6 and 13.7 for further details). Spectral information and band power extraction have been commonly used as features (see [82][81] for reviews); however, phase and cross frequency coupling less so even though a number of non-invasive and intracortical studies have emphasised the importance of phase information [32][36][103][104]. Furthermore, amplitude-phase cross-frequency coupling is suggested to play an important role in neural coding [105]. While neural representations of movement kinematics and movement imagination by amplitude information in sensorimotor cortex have been extensively reported using different oscillatory signals (LFP, ECoG, MEG, EEG) [32][36][40][106–108] and used extensively in non-invasive motor imagery based BCI designs phase information has not been given as much attention

as possibly deserved [36]. As reported in [36] there have been some recent developments describing synchronized activity between M1 and hand speed [80][81], corticomuscular coupling [111], and LFP Beta oscillations phase locked to target cue onset in a instructed-delay reaching task [112] in addition to the studies covered in sections 13.6 and 13.7 among others. The role of phase coding in sensorimotor cortex should be further explored to fully exploit the complementary information encoded by amplitude and phase [36].

Parameter optimization can be made more proficient through global searches of the parameter space using evolutionary computation based approaches such as practical swarm optimization (PSO) and genetic algorithms (GAs). The importance of features can be assessed and ranked for different tasks using various feature selection techniques using information theoretic approaches such as partial mutual information (PMI) based input variable selection [97][113]. Parameter optimization and feature selection approaches such as these enable coverage of a large parameter space when additional features are identified to enhance performance. Heuristic based approaches can be used to determine the relative increase in classification associated with each variable along with other more advanced methods for feature selection such as Fisher's criterion and partial mutual information to estimate the level of redundancy among features. Verifying the feature landscape using global heuristic searches is important initially and automated intelligent approaches enable efficient and automated system optimization during application at a later time and easy application to a large sample of participant data i.e., removing the necessity to conduct global parameter searches.

13.9.2 Classification

Various classifier techniques can be applied to the sampled data to determine classification/prediction performance including standard linear methods such as linear discriminant analysis (LDA), support vector machines (SVM) and probabilistic based approaches [114] as well as nonlinear approaches such as backpropagation neural networks (NNs) and self-organizing fuzzy neural networks (SOFNN) [115]. Other adaptive methods and approaches to classifier combination have been investigated [116][86][87] along with Type-2 fuzzy logic approaches to deal with uncertainty [119][120]. Recent evidence has shown that probabilistic classifier vector machines (PCVM) have significant potential to outperform other tried and tested

classifiers [121][122]. These are just a few of the available approaches (see [81] for a more detailed review). Here we focus on one of the latest trends in BCI translation algorithms i.e., automated adaptation to non-stationary changes in the EEG dynamics over time.

13.9.3 Unsupervised Adaptation in Sensorimotor Rhythms BCIs

EEG signals deployed in BCI are inherently non-stationary resulting in substantial change over time, both within a single session and between sessions, resulting in significant challenges in maintaining BCI system robustness. There are various sources of non-stationarities: short-term changes related to modification to the strategy that users apply to motor imagery to enhance performance, drifts in attention, attention to different stimuli or processing other thoughts or stimuli/feedback, slow cortical potential drifts and less specific long term changes related to fatigue, small day to day differences in the placement of electrodes among others. However, one which is considered a potential source of change over time is the user adaption through motor learning to improve BCI performance over time, sometimes referred to as the effects of feedback training [123][124] and sensorimotor learning.

The effects of feedback on the user's ability to produce consistent EEG, as he/she begins to become more confident and learns to develop more specific communication and control signals, can have a negative effect on the BCIs feature extraction procedure and classifier. During sensorimotor learning the temporal and spatial activity of the brain continually adapts and the features which were initially suited to maximising the discrimination accuracy may not remain stable as time evolves thus degradation in communication occurs. For this reason the BCI must have the ability to adapt and interact with the adaptations that the brain makes in response to the feedback. According to Wolpaw et al [125] the BCI operation depends on the interaction of two adaptive controllers, the user's brain, which produces the signals measured by the BCI, and the BCI itself, which translates these signals into specific commands [125].

With feedback, even though classification accuracy is expected to improve with increasing number of experiments, the performance has been shown to decrease with time if the classifier is not updated [42]. This has been referred to as the "Man-Machine Learning Dilemma" (MMLD), meaning that the two systems involved (man

and machine) are strongly interdependent, but cannot be controlled or adapted in parallel [42]. The experiments shown in many studies show that feedback results in changing EEG patterns and thus adaptation of the pattern recognition methods is required. It is therefore paramount to adapt a BCI periodically or continuously if possible. Autonomous adaptive systems design is required but a challenge. The recognition and productive engagement of adaptation will be important for successful BCI operation. According to Wolpaw *et al.* [125] there are three levels of adaptation which are not always accounted for but have great importance for future adoption of BCI systems:

1. When a new user first accesses the BCI, the algorithm adapts to the user's signal features.
 - No two people are the same physiologically or psychologically therefore brain topography differs among individuals and the electrophysiological signals that are produced from different individuals are unique to each individual, even though they may be measured from the same location on the scalp whilst performing the same mental tasks at the same time. For each new user the BCI has to adapt specifically to the characteristics of each particular person's EEG. This adaptation may be to find subject-specific frequency bands which contain frequency components that enable maximal discrimination accuracy between two mental tasks or train a static classifier on a set of extracted features.
2. The second level of adaptation requires that the BCI system components be periodically adjusted or adapted online to reduce the impact of spontaneous variations in the EEG.
 - Any BCI system which only possesses the first level of adaptation will continue to be effective only if the user's performance is very stable. Most electrophysiological signals display short and long term variations due to the complexity of the physiological functioning of the underlying processes in the brain among other sources of change as outlined above. The BCI system should have the ability to accommodate these variations by adapting to the signal feature values which maximally express the user's intended communication.

3. The third level of adaptation accommodates and engages the adaptive capacities of the brain.

- The BCI depends on the interaction of two adaptive controllers, the BCI and the user's brain. "*When an electrophysiological signal feature that is normally merely a reflection of brain function becomes the end product of that function, that is, when it becomes an output that carries the user intent to the outside world, it engages the adaptive capacities of the brain*" [125]. This means that, as the user develops the skill of controlling their EEG, the brain has learned a new function and hopefully the brain's new learned function will modify the EEG so as to improve BCI operation. The third level of adaptation should accommodate and encourage the user to develop and maintain the highest possible level of correlation between the intended communication and the extracted signal features that the BCI employs to decipher the intended communication. Due to the nature of this adaptation (the continuous interaction between the user and the BCI) it can only be assessed online and its design is among the most difficult problems confronting BCI research.

McFarland et al. [126] further categorise adaptation into system adaptation, user adaptation, and system and user co-adaptation, asking the question: is it necessary to continuously adapt the parameters of the BCI translation algorithm? Their findings show that for sensorimotor rhythms BCI it is, whereas perhaps not for other stimulus based BCIs.

A review of adaptation methods is included by Hasan [127] focusing on questions: what, how, and when to adapt and how to evaluate adaptation success? A range of studies have been aimed at addressing the adaptation requirements [118] [123][124][128][129][130][131][132][133][134][135][136]. Krusienski et al. [36] define the various types of possible adaptation as follows:

Covariate Shift Adaptation/Minimisation- *Covariate shift* refers to when the distribution of the training features and test features follow different distributions while the conditional distribution of the output values (of the classifier) and the features is unchanged [137]. The shift in feature distribution from session to session can be significant and can result in substantive biasing effects. Without some form of

adaption to the features and/or classifier, the classifier trained on a past session one would perform poorly on more recent session. Satti et al. [138] proposed a method for covariate shift minimization covariate (CSM) where features can be adapted so that the feature distribution is always consistent with the distribution of the features that were used to train the classifier in the first session. This can be achieved in an unsupervised manner by estimating the shift in distribution using a least squares fitting polynomial for each feature and removing the shift by adding the common mean of the training feature distribution so that the feature space distribution remains constant over time as described in [138]. Mohammadi et al. [139] applied CSM in self-paced BCI updated features to account for short terms (within trial) drifts in signal dynamics. In [137] an importance weighted cross-validation for accommodating covariate shift under a number of assumptions is described but is not adaptively updated online in an unsupervised manner whereas other offline approaches have been investigated to enable feature extraction methods to accommodate non-stationarity and covariate shifts [89][90].

Feature Adaptation/Regression - involves adapting the parameters of the feature extraction methods to account for subject learning e.g., modifying the subject-specific frequency bands can be easily achieved in a supervised manner but this is not necessarily easily achieved online, unsupervised. An approach to adaptively weight features based on mu and beta rhythm amplitudes and their interactions using regression [140] resulted in significant performance improvements and may be adapted for unsupervised feature adaptation.

Covariate Shift Adaptation/Minimisation can be considered an *anti-biasing* method because it prevents the classifier biasing whereas *Feature Adaption/Regression* is likely to result in the need to adapt the classifier to suit the new feature distributions. Both methods help to improve the performance over time but it is uncertain if Feature Adaption followed by *Covariate Shift Minimisation* (to shift features towards earlier distribution) would limit the need for classifier adaptation and/or provide stable performance or negate the benefits of feature regressions. An interesting discussion on the interplay between feature regression and adapting bias and gain terms in the classifier is presented in [140].

Classifier Adaptation - Unsupervised classifier adaptation has received more attention than feature adaptation with a number of methods proposed [118], [124].

Classifier adaptation is required when significant learning (or relearning) induced plasticity in the brain significantly alters the brain dynamics resulting in a shift in feature distribution as well as significant changes in the conditional distribution between features and classifier output as opposed to cases where only covariate shift has occurred. In such cases classifier adaptation can neither be referred to as anti-biasing or de-biasing.

Post Processing Adaptation - de-biasing the classifier output, in its simplest form, can be performed in an unsupervised manner by removing the mean calculated from a window of recent classifier outputs from the instantaneous value of the classifier [141], also referred to as normalization in [142] where the data from recent trials are used to predict the mean and standard deviation of the next trial and the data of the next trial is then normalised by these estimates to produce a control signal which is assumed to be stationary. De-biasing is suitable when covariate shift has not been accounted for and can improve the online feedback response but may only provide a slight performance improvement.

EEG Data Space Adaptation (EEG-DSA) acts on the raw data space and is a new approach to linearly transform the EEG data from the target space (evaluation/testing session), such that the distribution difference to the source space (training session) is minimized [143]. The Kullback-Leibler (KL) divergence criterion is the main method deployed in this approach and it can be applied in supervised or unsupervised manner either periodically or continuously. Other adaptations (feature space or classifier) can be applied in tandem but accurate minimization of feature space adaptation should negate the need for further anti-biasing and or de-biasing adaptations.

Classifier Adaptation (anti-biasing) negates the need for Post Processing (de-biasing) if the classifier is updated continuously which is a challenging task to undertake in an unsupervised manner (with no class labels) and may results in mal adaptation whereas de-biasing can be conducted easily, unsupervised, regardless of the classifier used. Because post processing based de-biasing only results in removal of bias (shifts it to mean zero) in the feedback signal and not necessarily a change in the dynamics of the feedback signal, feature adaptation or classifier adaptation is necessary during to subject learning and adaptation as the conditional distribution between features and classifier output evolve as outlined above.

All of the above methods are heavily dependent upon the context in which the BCI is used. For example, for a BCI applied in alternative communication the objective is to maximise the probability of interpreting the users intent correctly therefore the adaptation is performed with that objective whereas, if the BCI is aimed at inducing neuroplastic changes in specific cortical areas, e.g., a BCI which is aimed at supporting stroke survivors perform motor imagery as means of enhancing the speed or level of rehabilitation post stroke, the objective is to not only provide accurate feedback but to encourage the user to activate regions of cortex which don't necessarily provide optimal control signals [36]. The latter may require electrode/channel adaptation strategies but not necessarily in a fast online unsupervised manner. Abrupt changes to classifier performance may also lead to negative learning where the user cannot cope with the rate at which the feedback dynamics change, in such cases consistent feedback, even though less accurate, may be appropriate. As outlined in [144] there is still debate around whether mutual adaptation of a system and user is a necessary feature of successful BCI operation or if fast adaptation of parameters during training is not necessary. A recent study in animal models suggests that that there is no negative correlation between decoding performance and the time between model generation and model testing, which suggests that the neural representations that encode kinematic parameters of reaching movements are stable across the months of study [145][146], which further suggests little adaptation is needed for ECoG decoding in animal models but this may not necessarily translate to humans and non-invasive BCIs involving motor imagery. Much more research on the issue of what type of adaption methods to apply and at what rate adaptation is necessary. Another important factor is considering a person level of ability to control a BCI and those close to chance level may actually benefit from an incorrect belief on their performance level [147]. This would imply adapting the classifier output based on knowledge of the targets in a supervised manner such that user thinks they are performing better – a method which may help in the initial training phases to improve BCI performance [147]. Most of the techniques outlined above have been tested offline and therefore there is need to assess how the techniques improve performance as the user and BCI are mutually adapted. Table 1 below provides a summary of the categories of adaptation and their interrelationships and requirements.

Table 1 lists a number BCI components that can be adapted and the way in which they can be adapted as well as the interrelationship between components i.e., indicating when one is adapted which others component or stages of the signal processing pipeline it might be necessary to adapt (whether a calibration session is needed for offline setup or there is certain number of trials needed before adaptation begins is not specified in the criteria but is another consideration)

Adaptation Type	Anti-Biasing	De-Biasing	Subject Relearning	Feature updates	Classifier Adaptation	Online	Supervised	Unsupervised	Performance Improvement Likely
Channel Adaptation			Y	Y	Y		Y		Y
Data Space Adaptation	Y					Y		Y	Y
Feature Regression	Y		Y	Y	Y	Y		Y	Y
Covariate Shift Minimization	Y			Y		Y		Y	Y
Covariate Shift Adaptation			Y		Y		Y		Y
Classifier Adaptation	Y		Y		Y		Y	Y	Y
Gain/Bias		Y						Y	Slight

13.9.4 BCI Outlook

Translating brain signals into control signals is a complex task. The communication bandwidth given by BCI is still lagging most other communication methods rates between humans and the external world where maximum BCI communication rate is approximately 0.41 bits/s (~25bits/min) [148] (see Figure 13.11 for an illustration which illustrates nicely the gap in communication bandwidth between BCI and other communication methods as well as the relatively low communication bandwidth across all human-human and human-computer interaction methods).

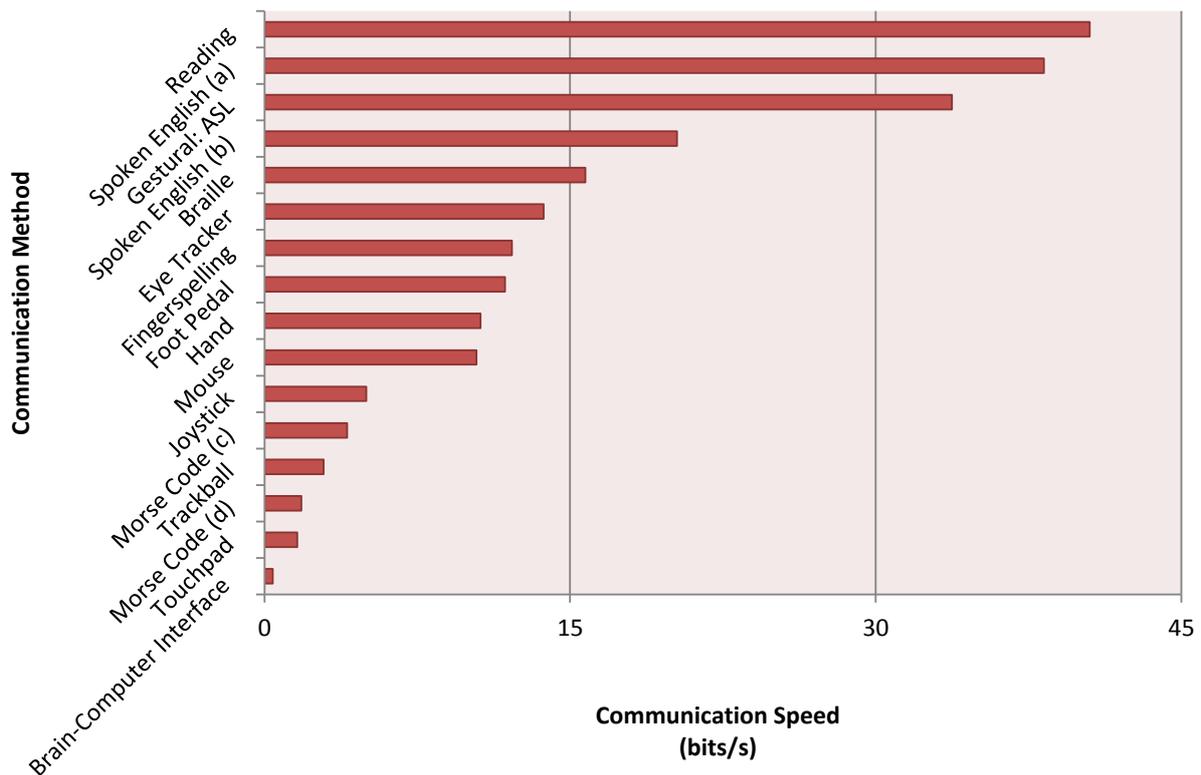


Figure 13.11 Comparison of communication rates between humans and the external world: (a) speech received auditorily; (b) speech received visually using lip reading and supplemented by cues; (c) Morse code received auditorily; (d) Morse code received through vibrotactile stimulation (Figure adapted from [148] with permission and other sources [107][108]).

Nevertheless with the many developments and studies highlighted throughout this chapter (a selected few among many) there has been progress, yet there is still debate around whether invasive recordings are more appropriate for BCI with findings showing that performance to date is not necessarily better or communications faster with invasive or extracellular recordings compared to EEG (see Figure 13.12 for an illustration [57]). As shown, performance is far less consistent than a joystick for 2D centre-out task using both methods, however the performance is remarkably similar even though the extracellular recordings are high resolution and EEG is low resolution. Training rates/durations with invasive BCI are probably less onerous on the BCI user compared to EEG based approaches which often require longer durations, however only a select few are willing to undergo surgery for BCI implants due to the high risk associated with the surgery required, at least with the currently available technology. This is likely to change in the future and

information transfer between humans and machines increase to overcome the communication bottleneck human-human and human-computer interaction by directly interfacing brain and machine [148]. There is one limitation that dogs many movement or motor related BCI studies and that is that in a large part control relies only a signal from single cortical area [57]. Exploiting multiple cortical areas may offer much more and this may be achieved more easily and successfully by exploited information acquired at different scales using both invasive and non-invasive technologies (many of the studies reported through this chapter have shown advantages that are unique at the various scales of recording). Carmena [3] recommends that non-invasive BCIs should not be pitted against invasive as both have pros and cons and have gone beyond pitching resolution as an argument to use one type or another. In the future BCI systems may very well become a hybrid of different kinds of neural signals, able to benefit from local, high-resolution information (for generating motor commands) and more global information (arousal, level of attention, and other cognitive states) [3].

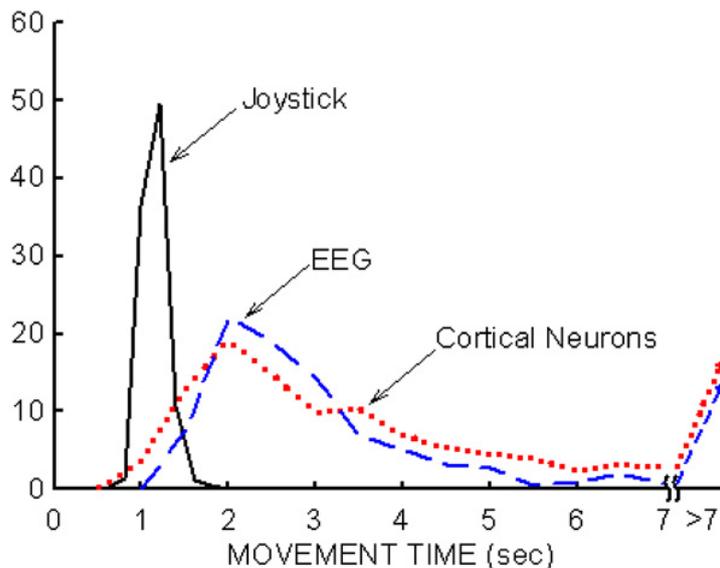


Figure 13.12 Distributions of target-acquisition times (i.e. time from target appearance to target hit) on a 2D center-out cursor-movement task for joystick control, EEG-based BCI control, and cortical neuron-based BCI control. The EEG-based and neuron-based BCIs perform similarly and both are slower than and much less consistent than the joystick. For both BCIs in a substantial number of trials, the target is not reached even in the 7s allowed. Such inconsistent performance is typical of movement control by present-day BCIs, regardless of what brain signals they use (The joystick data and neuron-based BCI data are from Hochberg et al. [151]. The EEG-based BCI data are from Wolpaw and McFarland [56]. Figure reproduced from McFarland et al. [57] with permission).

In summary, BCI technology is developing through better understanding of the motor system and sensorimotor control; better recording technologies, better signal processing, more extensive trials with users, long term studies, more multidisciplinary interactions among many other reasons. According to report conducted by Berger et al. [152] the magnitude of BCI research throughout the world will grow substantially, if not dramatically, in future years with multiple driving forces:

- Continued advances in underlying science and technology
- Increasing demand for solutions to repair the nervous system
- Increase in the aging population world-wide; need for solutions to age-related, neurodegenerative disorders, and for “assistive” BCI technologies
- Commercial demand for nonmedical BCIs

BCI has the potential to meet many of these challenges in healthcare and is already growing in popularity for nonmedical applications. BCI is considered by many as a revolutionary technology.

An analysis of the history of technology shows that technological change is exponential and according to the law of accelerating returns as the technology performance increase more and more users groups begin to adopt the technology and prices begin to fall [153]. In terms of BCI there has been significant progress over recent years and these trends are being observed with technology diffusion increasing [148]. In terms of research there is an exponential growth in the number of peer reviewed publications since 2000 [83].

Many studies over the past two decades have demonstrated that non-muscular communication, based on brain-computer interfaces (BCIs), is possible and, despite the nascent nature of BCIs there are already a range of products including alternative communication and control for the disabled stroke rehabilitation, electrophysiologically interactive computer systems, neurofeedback therapy and BCI controlled robotics/wheelchairs. A range of case studies have also shown that head trauma victims diagnosed as being in a persistent vegetative state (PVS) or minimally conscious state and patients suffering 'locked-in syndrome' as a result of motor neuron disease or brainstem stroke can specifically benefit from current BCI systems although, as BCIs improve and surpass existing assistive technologies, they will be beneficial to those with less severe disabilities. In addition, the possibility for enriching computer game play through BCI also has immense potential and

computer games as well as other forms of interactive multimedia are currently an engaging interface technique for therapeutic neurofeedback and improving BCI performance and training paradigms. Brain-Computer Games Interaction provide motivation and challenge during training which is used as stepping stone towards applications that offer enablement and assistance. Based on these projections and the ever increasing knowledge of the brain the future looks bright for BCIs.

13.10 Conclusion

The scientific approaches described throughout this chapter often overlook the underpinning processes, and rely on correlations between a minimal number of factors only. As a result, current sensorimotor rhythms BCIs are of limited functionality and allow basic motor functions (a two degrees-of-freedom (DOF) limited control of a wheelchair / mouse cursor / robotic arm) and limited communication abilities (word dictation). It is assumed that BCI systems could greatly benefit from the inclusion of multimodal data and multi-dimensional signal processing techniques which would allow the introduction of additional data sources, data from multiple brain scales and enable detection of more subtle features embedded in the signal. Furthermore, using knowledge about sensorimotor control will be critical in understanding and developing successful learning and control models for robotic devices and BCI and fully closing the sensorimotor learning loop to enable finer manipulation abilities using BCIs and for retraining or enabling better relearning of motor actions after cortical damage. As demonstrated throughout the chapter, many remarkable studies have been conducted with truly inspirational engineering and scientific methodologies resulting in many very useful and interesting findings.

There are many potential advantages of understanding motor circuitry, not to mention the many clinical and quality of life benefits a greater understanding of the motor systems may provide. Such knowledge may offer better insights into treating motor pathologies that occur as a result of injury or diseases such as spinal cord injury, stroke, Parkinson's disease, Guillain Barre Syndrome, motor diseases and Alzheimer's disease to mention just a few. Understanding sensorimotor systems can provide significant gains in developing more intelligent systems that can provide multiple benefits for humanity in general. However there are still lacunae in our biological account of how the motor system works.

Animals have superb innate abilities to choose and execute simple and extended courses of action and ability to adapt their actions to a changing environment. We are still a long way from understanding how that is achieved and exploiting this to tackle the issues outlined above comprehensively. There are number of key questions that need to be addressed:

- What are the roles of the cortex, the basal ganglia and the cerebellum – the three major neural control structures involved in movement planning and generation? [154]
- How do these structures in the brain interact to deliver seamless adaptive control? [154]
- How do we specify how hierarchical control structures can be learned? [154]
- What is the relationship between reflexes, habits and goal-directed actions? [154]
- Is there anything to be gained for robotic control by thinking about how interactions are organised in sensorimotor regions?
- Is it essential to replicate this lateralised structure in sensorimotor areas to produce better motor control in an artificial cognitive system?
- How can we create more accurate models of how the motor cortex works? Can such models be implemented to provide human-like motor control in an artificial system?
- How can we decode motor activity to undertake tasks which require accurate and robust three dimensional control under multiple different scenarios?

Wolpert et al. [15] elaborate on some of these questions, in particular, one which has not been addressed in this chapter, namely modelling sensorimotor systems. Although substantial progress has been made in computational sensorimotor control, the field has been less successful in linking computational models to neurobiological models of control. Sensorimotor control has traditionally been considered from a control theory perspective, without relation to neurobiology [155]. Although neglected in this chapter, computational motor cortical circuit modelling will be a critical aspect of research into understanding sensorimotor control and learning, and is likely to fill parts of the lacunae in our understanding which are not accessible with current imaging, electrophysiology and experimental methodology. Likewise, understanding the computations undertaken in many of sensorimotor areas will depend heavily on

computational modelling. Doya [156] suggested the classical notion that the cerebellum and the basal ganglia are dedicated solely to motor control is under dispute given increasing evidence of their involvement in non-motor functions. However, there is enough anatomical, physiological and theoretical evidence to support the hypotheses that the cerebellum is a specialised organism that may support supervised learning, the basal ganglia may perform reinforcement learning role, and the cerebral cortex may perform unsupervised learning. Paucity of alternative theories that enable us to comprehend the way the cortex, cerebellum and the basal ganglia participate in motor, sensory or cognitive tasks are required [156].

Additionally, as has been illustrated throughout this work, investigating brain oscillations is key to understanding brain coordination. Understanding the coordination of multiple parts of an extremely complex system such as the brain is a significant challenge. Models of cortical coordination dynamics can show how brain areas may cooperate (integration) and at the same time retain their functional specificity (segregation). Such models can exhibit properties that the brain is known to exhibit, including self-organization, multi-functionality, metastability and switching. Cortical coordination can be assessed by investigating the collective phase relationships among brain oscillations and rhythms in neurophysiological data. Imaging and electrophysiology can be used to tackle the challenge of understanding how different brain areas interact and cooperate.

Ultimately better knowledge of the motor system through neuroengineering sensorimotor-computer interfaces may lead to better methods of understanding brain dysfunction and pathology, better brain-computer interfaces, biological plausible neural circuit models and inevitably more intelligent systems and machines that can perceive, reason, and act autonomously. It is too early to know the overarching control mechanisms and exact neural processes involved in the motor system but through the many innovations of scientists around the world, as highlighted in this chapter, pieces of the puzzle are being understood and slowly assembled to reach this target and go beyond.

13.11 Bibliography

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13.12 Keywords

efference copy, motion primitives, motion smoothness, internal model, vectorial planning, forward models, inverse models, motion kinematics, feedback, feed-forward, minimum jerk hypothesis, EEG, ECoG, fMRI, MEG, brain oscillations, motor imagery, brain-computer interface, sensorimotor learning, explicit motor learning, implicit motor learning, extracellular recording, population vector, neural codes, co-articulation, movement cuing, diffusion tensor imaging