Preface

This Festschrift for Alf Zimmer focuses on new issues in experimental and applied psychology. Based on the pioneering research achievements of Alf Zimmer, the contributors to the Festschrift examine issues related to cognition and action planning.

Gerhard Roth introduces the reader to the complexities of the Human brain and the neural mechanisms underlying conscious and unconscious control of behavior. A variety of human motor responses - ranging from hard-wired reflexes to dynamic voluntary movements - are under the control of neural circuits. These neural circuits are multisynaptic, involving motor neurons, themselves under the influence of cortical and subcortical control loops. Roth addresses the issue of consciousness and how consciousness arises in the Human central nervous system. He focuses on the modular nature of consciousness: different neurocognitive processes contribute to different levels of conscious processing, including but not limited to awareness of our own body and body actions and an awareness of the reality of the world about us. Conscious arises as an emergent property of the complex interplay between the cerebral cortex including the limbic cortex and subcortical structures. The study of the neural mechanisms underlying Human consciousness sets the stage for the scientific study of Human cognition and action control.

Karl-Heinz Bäuml focuses on the cognitive and neurocognitive mechanisms underlying retrieval from human episodic memory. For a long time, memory retrieval was regarded as a relatively neutral event that, more or less successfully, „reads out" information from memory storage. Research from the past decades, however, revealed that selective retrieval from episodic memory is not a neutral event and can have quite severe detrimental effects on related memories. This finding was termed retrieval-induced forgetting and was found to be a very general and robust phenomenon. Building on ideas from applied psychology in the area of eyewitness testimony, Bäuml describes recent experimental work from his laboratory and from those of others on retrieval-induced forgetting. Reviewing 15 years of research, Bäuml summarizes experimental evidence for the view that retrieval induced forgetting is caused by inhibitory executive-control processes in human memory. In addition, the effects of emotion on retrieval-induced forgetting are considered, as well as the neural mechanisms mediating the forgetting and the development of the inhibition over the individual lifespan.

Josef Krems and Martin Baumann focus on the study of action control behind the steering wheel. Driving is a complex neurocognitive task that requires situation awareness on the part of the driver, who is in control of the vehicle in traffic. With over 3000 moralities per day, driving is a risky business. The study of driver's behavior and cognitive control of driving is fundamental to the design of roads and road safety. Here the authors focus on the concept of situational awareness as an adaptive form of controlled consciousness. Building on the work of Neisser in the 1970's and Endsley in the 1990's, Krems and Baumann define situational awareness as the state of knowledge and the cognitive processes leading to this state of knowledge. Mental models or schemata are used by the driver to interpret the momentary driving scenario, thereby allowing for the preparation and execution of appropriate behavioral control of the moving vehicle. How these situation models are constructed, maintained and updated is a major focus of this chapter. The interaction between the driver's situational models and intelligent assistive systems within the car form an important bridge from basic cognitive to applied research.

Together with Michael Schrauf and James Thomas, the editor of this volume looks at the neurocognitive mechanisms that underlie the effects of workload on cognitive processes. Stimulus uncertainty contributes to workload, since uncertainty about the time, spatial location or nature of stimuli increasing our need to monitor several channels of sensory information at once. Signal detection theory provides us with tools to study the effects of workload and stimulus uncertainty on discrimination performance. Human cognition is a limited capacity information-processing system that requires selection among different information sources. This selection process is referred to as attention. Neurocognitive approaches study the effects of workload on performance and brain activity using stimulus discrimination, simulated driving and visual working memory tasks. Modern brain imaging techniques can be employed to determine the effects of workload on task-related neural responses in specific regions of the human brain. We describe a neurocognitive approach to research on the effects of workload in simulated (laboratory) and real (field) experiments. The findings suggest that functional brain imaging can provide important new insights into the way operators perform challenging tasks. The transfer to real driving scenarios is achieved by recording EEG activity from the driver's brain while he or she reacts to real events on the road.

Christhard Gelau describes the applied research concerning elderly drivers and road safety. Age-related deteriorations of driving-relevant skills and abilities constitute an important issue demanding empirical research to uncover the factors that may lead to an increased risk in elderly drivers. Driving maneuvers at intersections turn out to be particularly hazardous for elderly drivers, which might be related to age-related error proneness especially when the driver makes a left turn. Empirical research in different countries is reviewed and experimental results from a driving simulator study are presented, which was performed to evaluate the benefits of an assistance function specifically designed to support the elderly.

Hermann Körndle, Susanne Narciss and Antje Proske describe their work on web-based learning and instruction tools. Web-based learning scenarios and the Web-LEs provide access to instructional materials and media. The authors discuss the reasons why web-based learning scenarios are not used more in educational institutions. Web tools such as the Exercise-Format-Editor (EF-Editor), the Study-to-Web Compiler (s2w-compiler) and the electronic exercise TEE-machine are presented in detail. The authors go on to discuss the factors underlying the design and evaluation of web-based learning environments. The concept of learners-as-designers is discussed and it possible application in higher-level educational setting is considered. The authors review the research results on the use of web-based learning tools in different settings.

Klaus Lange, Thomas Sontag, Dorota Stasik, Lara Tucha and Oliver Tucha present new results concerning their experimental research on graphomotor abilities. Spatial and kinematic properties of handwriting can be acquired using digitizing tablets. Kinematic aspects of handwriting can provide important insights into the cognitive and motor control of skilled movements. The authors discuss several factors that influence the production of automatic handwriting movements. The effects of impaired attention on handwriting in children with attention deficit hyperactivity disorder (ADHD) are considered. Parkinson's disease is also associated with

characteristic changes in handwriting and the effects of this neurodegenerative pathology on handwriting is explored, along with the effects of acute phenylalanine and tyrosine depletion in healthy volunteers. A review of research on the central dopaminergic mechanisms involved in the control of handwriting is given.
The final chapter by Hans Gruber, Jörg Marienhagen, Eckart Altenmüller focuses on the physiological and neural adaptations occurring during the acquisition of expertise. Excellent performance associated with expertise appears to be restricted to the domain of the expertise itself, suggesting a specific form of neural plasticity. The authors discuss different research strategies used to explore changes that come about in association of the acquisition of expertise. Applications in the area of professional expertise provide an important extension of this basic research approach. The role of eye movements in expert radiologists who examine medical images is a pertinent example of how expertise can change behavior. Research on the neural correlates of expertise acquisition is discussed and different approaches are compared. Alterations in the function and structure of the brains of expert musicians are examples of this compelling work. The authors conclude that brain plasticity occurs over different time spans from seconds, minutes, hours, days, months and years. The application of neuroscientific method to learning and education provides exciting and novel insights into how our brains adapt to the ever-changing demands placed on us by society.

This *Festschrift* provides an excellent introduction to current research in these different areas with a strong focus on the contributions from the University of Regensburg and cooperating institutions.

Mark Greenlee
Regensburg, June 2009

Conscious and Unconscious Control of Behavior

Gerhard Roth

1. Introduction

Human motor responses are of the following types: (1) voluntary and deliberate actions, (2) automatic actions such as writing, typing with a keyboard, riding a bicycle or playing a piano, (3) responses to affective-emotional stimuli, (4) rhythmic-involuntary actions such as breathing, chewing, and walking, and (5) reflexes such as withdrawal reactions or orienting responses and reflex-like behavior such as the control of body posture (Jeannerod, 1997).

Reflexes, reflex-like behaviors and rhythmic-involuntary actions are controlled by circuits and centers in the spinal cord and brainstem, and they are not bound to consciousness. These kinds of behavior are either completely inborn, or training and learning of the motor activity take place at early childhood, e.g. in the context of walking on two legs or grasping an object. Responses to affective-emotionally arousing stimuli are influenced by learning and experience, but they often likewise occur without any awareness, for example in the case of early childhood experience during the period of "infantile amnesia" or of unconscious emotional conditioning. Automatic actions are likewise largely independent of consciousness, i.e. we do not need to pay attention to them, while we execute them. Finally, voluntary actions exhibit the highest degree of plasticity and dependence on attention, learning and experience.

All this raises the question why some kinds of behavior are accompanied by consciousness and others are not.

2. Phenomenology and Neuronal Basis of Consciousness

In humans, consciousness includes very different phenomena which only have in common the fact that we have subjective awareness of them and that we can – at least in principle – report them (Roth, 2000, 2003). States of consciousness include *conscious perception* of events happening in the world around me and within my body, which differ in modality, submodality (quality), quantity, intensity, location in space and time, content and meaning. *Mental activities* such as thinking, self-reflection, remembering, imagining and planning are another class of specific states of consciousness and are usually felt differently from perceptions, as is the case with *emotions* (Tsuchiya and Adolphs, 2007). *Attention* is a state of increased and focused consciousness. It can be driven externally or internally. In the latter case, it goes along with improved perceptual abilities (e.g., increased visual acuity or lowered auditory threshold) (Kolb and Wishaw, 1993).

These states of consciousness together form "actual consciousness" and differ from what is called "background consciousness". This includes *body-identity awareness*, i.e. the belief that I belong to the body that apparently surrounds me, *autobiographic consciousness*, i.e. the conviction that I am the one who existed yesterday, *reality awareness* of what was going on in the past and is happening in the world surrounding me, awareness of *voluntary control of movements and actions*, of *being the author of my thoughts and deeds*.

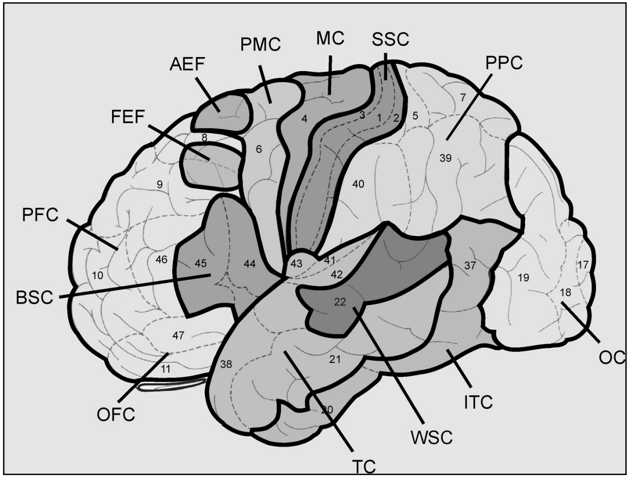
There is strong evidence for a *modular* organization of consciousness in the sense that different aspects of consciousness can dissociate, i.e., they can be impaired selectively after damage of restricted parts of the brain. There are patients who have normal states of cognition, consciousness and intelligence except that they deny that this is their own body or who do not know *who* or *where* they are (Kolb and Wishaw, 1993). Furthermore, different states of consciousness interfere only little with each other, if they are dissimilar in their general nature (perceptions vs. thoughts vs. emotions) or in their modality or semantic content. We can have emotions or thoughts while perceiving something, and in the same way we can watch the traffic on the street while listening to a Mozart symphony.

Consciousness is intimately bound to activities in the cerebral cortex (Smythies, 1997; Roth, 2000; Crick and Koch, 2003; Seth et al., 2008). This includes the so-called limbic (i.e. orbitofrontal-ventromedial, anterior cingulate and insular) cortex and the associative (parietal) and executive (prefrontal) cortex (Figure 1 and 2).

The limbic cortex exhibits a three-to-five-layered laminar organization, as opposed to the six-layered neo- or isocortex (Nieuwenhuys et al., 1988). The *orbitofrontal* and *ventromedial prefrontal cortex* (OFC, vmPFC) occupy the ventral and ventromedial part of the frontal cortex (Rolls, 1999). The major functions of these two closely related areas include conscious perception of emotions, emotional preparation and motivation of actions, assessment of consequences of one‘s own behavior and of individual and social risks, identification of the emotional expression and of the meaning in the actions of others (empathy), and learning and control of socially adequate behavior (Hornak et al., 2003; Uddin et al., 2007). OFC and vmPFC exert an inhibitory control of subcortical limbic centers, above all the amygdala (see below). Accordingly, deficits in these regions result in impulsive, egoistic and socially incorrect behavior, as can be seen in violent criminals (Raine et al., 1997; Anderson et al., 1999; Coccaro et al., 2007).

The *anterior cingulate cortex* (ACC) is situated in the medial frontal cortex posterior to but contiguous with the vmPFC. It consists of a dorsal cognitive and a ventral emotional-limbic subregion. Functions of the dorsal ACC include the control of externally and particularly internally driven attention and error monitoring, while the ventral ACC is involved in processing of affective and emotional components of pain perception, evaluation of reward and punishment, emotional assessment of future rewards and risks, and control and retrieval of emotional memories (Ullsperger and von Cramon, 2003; Botvinick et al., 2004; Rushworth and Behrens, 2008). The ACC is closely linked to subcortical limbic centers such as the amygdala and the mesolimbic system (see below).

The *insular cortex* (IC) is situated inside a deep folding of the cortex behind the so-called “operculum”. Its functions are the processing of gustatory and visceral stimuli (posterior IC), processing of affective and emotional components of pain sensation (Wiech et al., 2008) and identification of emotional content and meaning in the action of others, or empathy (anterior



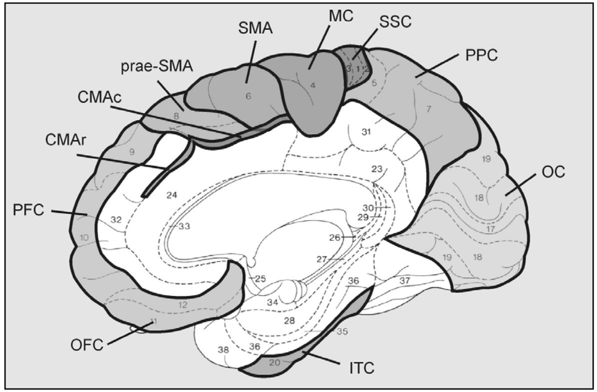


Fig. 1: (left): Functional anatomical division of the lateral surface of the cerebral cortex. The numbers refer to the cytoarchitectonic areas defined by K. Brodmann. Abbreviations: AEF = anterior eye field; BSC = Broca speech center; FEF = frontal eye field; ITC = inferior temporal cortex; MC = motor cortex; OC = occipital cortex; OFC = orbitofrontal cortex; PFC = prefrontal cortex; PMC = dorsolateral premotor cortex; PPC = posterior parietal cortex; SSC = somatosensory cortex; TC = temporal cortex; WSC = Wernicke speech area. (after Nieuwenhuys et al., 1991). (right) mesial surface of the cerebral cortex. Abbreviations: CMAc = caudal cingulate motor area; CMAr = rostral cingulate motor area; ITC = inferior temporal cortex; MC = motor cortex; OC = occipital cortex; OFC = orbitofrontal cortex; prae-SMA = prae-supplementary motor area; PFC = prefrontal cortex; PPC = posterior parietal cortex; SMA = supplementary motor area; SSC = somatosensory cortex. (Adapted from Nieuwenhuys et al., 1988).

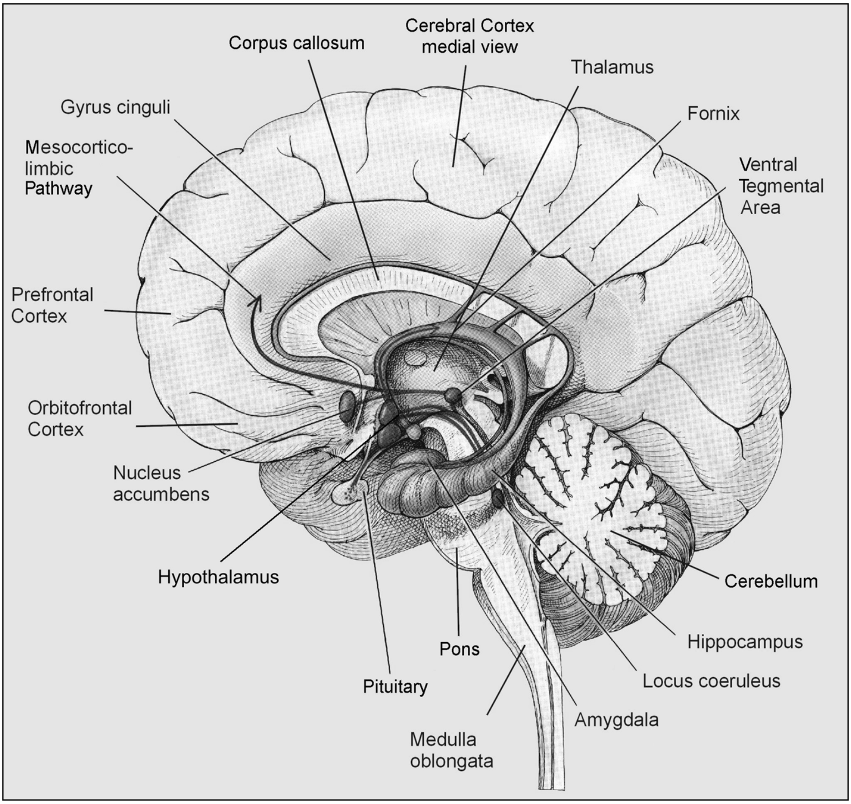


Fig. 2: Longitudinal section through the human brain with the most important limbic centers. These can be divided into areas responsible for the processing of positive (nucleus accumbens, ventral tegmental area) and negative affects (amygdala), for the organization of memory (hippocampus), for the control of attention and conscious processing (basal forebrain, locus coeruleus, thalamus) and for the control of autonomic functions (hypothalamus). (Adapted from Roth, 2003).

IC). The IC likewise is closely connected with subcortical limbic centers, predominantly the amygdala.
Taken together, these cortical limbic areas represent conscious affective and emotional components of awareness and particularly the expected positive or negative consequences of one's imagined or planned actions.
A special part of the limbic cortex is the three-layered *hippocampal formation* (Ammon´s horn, subiculum, dentate gyrus) and the surrounding five-layered entorhinal, parahippocampal and perirhinal cortex. These parts, in strong interaction with limbic thalamic nuclei and the prefrontal cortex, are important centers for the formation and the consolidation of traces of declarative memory inside the cortex, i.e., of those kinds of memory that in principle can be consciously retrieved and reported (Squire, 1987; Tulving and Markowitsch, 1998; Aggleton and Brown, 2006; Mayes et al., 2007)
The six-layered *neo- or isocortex* is composed of primary and secondary sensory (i.e. visual, auditory, somatosensory and vestibular) and motor-premotor cortices and the temporal, parietal and frontal-prefrontal associative cortex (Creutzfeldt, 1983). According to present evidence the activity of the sensory and motor cortices are not accompanied by consciousness, although they are necessary for its origin.
The *associative cortex* is involved in higher-order processing of information coming from primary and secondary sensory areas and from subcortical limbic centers. It includes the *posterior parietal cortex* (PP). The left PP is involved in symbolic-analytic information processing, mathematics, language, and interpreting drawings and symbols. Lesions impair reading and writing and respective memory functions. The right PP deals with real and mental spatial orientation, the control of hand and eye movement, change of perspective and control of spatial attention (Kolb and Wishaw, 1993; Husein and Nachev, 2007). The associative *superior* and *middle temporal cortex* houses perception of complex auditory stimuli including (generally left side) Wernicke´s semantic speech center, which is crucial for the understanding and the production of meaningful written and spoken language. Perception of music involves the left and right medial temporal cortex depending on different subtasks. The *inferior* temporal cortex (IT) is decisive for complex visual information regarding non-spatial properties of visual

objects and scenes along with their meaning and correct interpretation (Kolb and Wishaw, 1993).
The *prefrontal cortex* (PFC) represents the largest portion of the human cortex. Two major parts are distinguished in the primate, including human, brain: a dorsolateral and an orbitofrontal-ventromedial portion (Petrides and Pandya, 1999; Fuster, 2002). The latter is of limbic nature and has already been described. The *dorsolateral* prefrontal cortex (dlPFC) is involved in attention and selective control of sensory experience, action planning and decision-making, temporal coding of events, judgement and insight, spontaneity of behavior, strategic thinking, associative thinking, and working memory (Botvinick, 2004; McNab and Klingberg, 2007; Badre, 2008). Thus, the dlPFC is predominantly, though not exclusively, oriented toward the external world and its demands including short-term or working memory. It is viewed to monitor and adjust one´s behavior confidently and to be aware of one´s consciousness, thus exerting supervisory functions. Lesions of the dorsolateral PFC result in diminished intelligence, perseveration and impairment of making appropriate cognitive or behavioral switches.
The *supplementary motor area* (SMA) belongs to the frontal cortex and is situated between the medial aspect of the motor cortex and the dorsomedial prefrontal cortex; it represents a sort of associative motor cortex. It is active during the preparation and planning of complex movements and even during imagined movements. Together with the prefrontal cortex, it contributes to the awareness of being the author of one´s own deeds; accordingly, it was believed by some philosopher-neuroscientists to be the seat of "free will" (Eccles, 1982; Haggard 2005; Haggard et al. 2002).
General functions of the associative cognitive and executive isocortex are detailed perception, processing of large, multimodal data sets, semantically „deep" information processing including language, internal control of attention, fast comprehension of behaviorally relevant events, medium and long-range action planning and finally formation of secondary representations (thoughts, imaginations) including self-consciousness.
In summary, different parts of the associative cortex contribute in different ways to the high diversity and content of consciousness including awareness of external and internal sensory events, consequences of one´s own be-

havior, autobiographic, body and ego identity, action planning and authorship of one´s own deeds.

3. Subcortical Centers Involved in the Control of Behavior

The activity of subcortical centers is strictly unconscious, regardless of how complex this activity is and how deeply it influences the activities of the cortex. Here, we have to distinguish between three major subsystems, i.e. (1) subcortical *limbic* centers, predominantly amygdala and mesolimbic system, (2) *basal ganglia* and (3) the *autonomic system* in a larger sense including the preoptic-hypothalamic region and autonomic centers in the brainstem (Figure 2).

The *amygdala* is a complex of different nuclei and is reciprocally connected with the associative cortex, particularly the orbitofrontal cortex, either directly or via the mediodorsal thalamic nucleus, and with the hippocampal formation (Nieuwenhuys et al., 1988). Its major functions are the processing of olfactory and pheromonal information *(corticomedial amygdala)*, processing of gustatory, autonomic and visceral information, control of innate affective responses and simple emotional conditioning *(central amygdala)* (Panksepp, 1996; LeDoux, 1996; Samson and Paré, 2005), and finally processing of emotional communicative stimuli such as faces, gestures and speech as well as complex emotional conditioning *(basolateral amygdala)* (Aggleton, 2000; LeDoux, 2000; Swanson and Petrovitch, 1998). Lesions of the amygdala may lead to deficits in negative emotional conditioning, recognition of socially relevant emotional signals and impaired punishment sensitivity, i.e. reduced recognition of negative consequences of one's own deeds (Coccaro et al., 2007).

Importantly, the different parts of the amygdala influence behavior in different ways. First, the corticomedial and central amygdala influence the hypothalamic-autonomic system directly and release reflex-like and autonomic responses (LeDoux, 1996, 2000). Second, the basolateral and central amygdala influence the basal ganglia and in this way all automatic as well as deliberate actions (see below). Finally, the basolateral amygdala strongly influences the limbic cortex eliciting conscious emotions; it influences the hippocampus by emotionally modulating the storage and retrieval of memories, and the isocortex by modulating cognitive-executive tasks such as action planning and decisions (Passingham, 1993; LeDoux, 1996).

The *mesolimbic system* consists of the ventral tegmental areal, the nucleus accumbens/ventral striatum and the ventral pallidum. It is characterized by the neuromodulator dopamine (Berridge, 2007). Its major functions are the control of motivational and hedonic states, the control of active search for reward, representation of reward value, probability, expectations and monitoring (Schultz 2007; Goto and Grace, 2008). Deficits in the mesolimbic-dopaminergic system lead to anhedonia and lack of motivation. The mesolimbic system influences the basal ganglia, amygdala, hippocampus and the limbic cortex and isocortex in the same way as does the amygdala (Grace et al., 2007).

The third system to be mentioned is represented by the *dorsal basal ganglia*, i.e. the putamen, nucleus caudatus, globus pallidus, nucleus subthalamicus and substantia nigra (Nieuwenhuys et al., 1988; Graybiel et al., 1994; Jeannerod, 1997). These parts are closely associated via thalamic nuclei with the prefrontal, premotor and parietal cortex as well as with the entire limbic system. The basal ganglia represent a kind of „action memory“ in the sense that all voluntary movements that have been repeatedly and successfully executed are stored here. Before a new voluntary movement is executed, it must be sent from the cortex to the basal ganglia for compliance with this action memory. Likewise, the basal ganglia are the seat of all stereotyped actions and of habits, which typically can be exerted without conscious control. The basal ganglia are under strong control of the amygdala and the mesolimbic system and in this manner by unconscious emotional memory (McHaffie et al., 2005; Grillner et al., 2005)

4. Which Tasks Require Consciousness and Attention and which don’t?

Many, if not most, things of our daily life we execute in an automatic way, e.g., entering data or text on a computer keyboard, riding a bicycle or driving our car along a familiar route, all of which is at best only accompanied by awareness. However, such functions typically require attention, when we start learning them, but with increasing practice conscious attention becomes less and less necessary. There are ways of unconscious processing of sensory information, e.g., identification of meaningful objects. Of greatest importance in this context is the fast and unconscious recognition of emotionally relevant events such as threatening objects, fearful, angry or happy faces and gestures, which can take place within a fraction of a second and strongly influence our autonomic nervous system and our behavior (e.g., flight and fight). However, the unconscious processing of such events is typically based on salient features excluding the perception of details such as the "fearfulness" or "angriness" of a face. There is *implicit*, i.e., unconscious learning, e.g., of syntactical rules, but people typically remain unaware of what and how they have learned. The same is true for emotional conditioning, which can occur, while people are completely unaware of it. At the same time, it is impossible to process detailed and complex information that afterwards can be reported, without being attentive, e.g., grasping the meaning of a hitherto unheard sentence or comparing two complex pictures, to plan a complicated sequence of actions or to acquire a new complex motor skill, e.g., learning to play the piano or skating. In summary, everything that can be done *effortlessly*, does not require attention, while all *effortful* tasks need to be accompanied by awareness and attention. Also, unattended or poorly attended information is poorly recollected.

How, then, can we understand, why some information is processed and some actions are exerted unconsciously or with only accompanying attention, while other information and execution of actions requires consciousness?

To answer this question we have to keep in mind that the cerebral cortex, as the seat of consciousness, is a gigantic associative network consisting of about 15 billion (1.5×10^{10}) neurons, mostly pyramidal cells, and about 500 trillion synapses (5×10^{14}). Each pyramidal cell is connected to an average of 20-30.000 other pyramidal cells (Creutzfeldt, 1983). Most cortical synapses can change their conductivity (i.e. become more excitatory or more inhibitory) within a time window of 0.3-3 seconds. As a consequence, cortical networks are highly plastic and can alter the way they process information much faster than subcortical networks. At the same time, they have a much higher processing capacity for detailed information and for multiple perceptual, cognitive and executive representations. Subcortical networks lack these abilities.

However, the cortex pays for these important abilities by being metabolically costly in terms of oxygen and glucose consumption. While the brain, in its resting state, already consumes up to 20% of body metabolism, the cerebral cortex consumes up to ten times more oxygen and glucose than subcortical centers during states of high attentional load (Magistretti, 1999; Magistretti et al., 1999). In addition, cortical processing is slow and error-prone, while subcortical processing is fast, economic and efficient.

One of the most severe problems of the human brain is the "energy problem": In terms of its metabolic capacities, it is at the upper limit, because it is very large compared to body size. As a consequence, humans can be in a state of high attention and concentration for only a few minutes. In order to save energy, the human brain tries to avoid high cortical conscious activity whenever this is possible. This is done in the following way.

Any incoming sensory information is first evaluated unconsciously and in a "quick-and-dirty" way by subcortical brain centers, mostly by nuclei of the reticular formation, thalamus, limbic system and of allocortical hippocampus (Kumaran and Maguire, 2009), regarding two pairs of criteria, viz., "familiar-unfamiliar" and "important-unimportant", and this check of information lasts only about 100 ms. If an information is classified as "unimportant", it is excluded from further processing. If it is classified as "important" under cognitive or emotional aspects and also as "familiar", then the brain searches for pre-established actions programs within the limbic system and the basal ganglia for appropriate autonomic-affective responses or motor actions. These are then executed in a fast and effective manner either in a completely unconscious manner or with only accompanying awareness, which typically comes 0.5-1 seconds later. This may concern quick recognition of emotionally relevant events by the amygdala or the mesolimbic system such as threatening objects, faces, gestures, shouts, which release reactions such as fight, flight, defense, anger and pleasure. For example, we may respond to a threatening event by flight or defense (e.g. when confronted with a poisonous snake), before we know, why we are running away (LeDoux, 1996).

Similarly, highly stereotyped motor actions such as moving lips while talking or finger movements while piano playing, riding a bicycle, shifting gears while car driving or skillfully using an instrument is based on the activation of specialized action programs inside the basal ganglia in interaction with the primary motor cortex and the cerebellum (Krakauer and Shadmehr, 2006). As already mentioned, this usually takes place without focused attention, which – in contrast – would disturb the execution of the motor reaction, i.e., we should avoid thinking about how to move our finger while playing the piano.

Only if information is regarded as "important" and "unfamiliar" and for which the brain has no pre-established way of processing and reacting, this information is sent to the limbic and the associative-cognitive cortex. The task of this kind of cortex, then, is to form new networks by combining existing memory contents in a new and creative way to solve problems of recognition of objects, understanding spoken or written sentences or action planning (DeBello, 2008). This is a complex, time- and energy-consuming process, which, however, can be done only by cortical networks. In this sense, the cortex is a tool that is used by our brain, whenever problems are sufficiently new, important and complex.

However, if we are again confronted with the same kind of problems, our responses become faster and more effective, and this is accompanied by the fact that the respective motor sequences gradually shift from the cortex to the basal ganglia-cerebellar system, until these subcortical centers exert the motor program independent of the cortex except the primary motor cortex, which is always involved, when fine finger, lip etc. movements are required. Accordingly, consciousness is gradually withdrawn from the execution of these reactions; typically, at the same time such functions become more and more emotionless and meaningless. Apparently, the respective motor sequences are stored inside the basal ganglia in a highly compressed fashion, which may explain, why it is difficult to interfere intentionally "in the middle" of such a sequence.

5. Four Systems of Action Control

On the basis of the information presented so far, we recognize four different systems of action control in the brain besides mere reflex behavior which mostly involves the spinal cord and the lower brainstem. The most basic system comprises fast, involuntary and highly inborn responses of the autonomic system, including affective states (rage, anger, sexuality, fight, flight), which are controlled by the preoptic-hypothalamic region and the central and corticomedial amygdala as an essential component of the elementary "survival system". The second system is composed of unconscious, but largely experience-dependent emotional behavior controlled by the amygdala and the mesolimbic system (Dolan, 2000). This system, together with the first one, starts evaluating continuously, even before birth, what is "good" and "bad" for us, and stores the outcomes in our *unconscious emotional memory*. As discussed above, this memory influences all willed actions either directly via the cortex and hippocampus or indirectly via the basal ganglia.

The third system comprises all automatic actions mentioned above and is executed by the basal ganglia, the cerebellum and the primary motor cortex. It is influenced by the subcortical emotional centers and at least partly by the limbic cortex and isocortex which may give the "start command" for automatic motor programs. For example, our conscious cortex gives the command "start riding the bicycle", but the basal ganglia (plus cerebellum) determine *how* this is done.

The fourth system comprises all "willed" actions, be they spontaneous or planned. These actions are based on the activity of the limbic cortex and the isocortex. It controls all voluntary actions mostly via the pyramidal tract running from the cortex to motor centers in the brainstem and spinal cord (Passingham, 1993; Jeannerod, 1997). These actions are usually accompanied by consciousness and the feeling "I wanted this!" However, while each of the former three systems can act independently of the other systems, the fourth, cortical system is not independent of these other centers, as illustrated in Figure 3.

First, all emotions, wishes, desires and plans, which we experience consciously, become conscious in the cortex, predominantly in the pre- and orbitofrontal and parietal cortex, but this happens under the influence of the subcortical limbic system (Clore and Huntsinger, 2007). The conscious cortical system then reflects and evaluates these emotions, wishes, desires and plans and their alternatives and consequences, and eventually forms an *intention to act*. But 1-2 seconds before these intentions become an "act of will", they are finally checked by the basal ganglia under the influence of

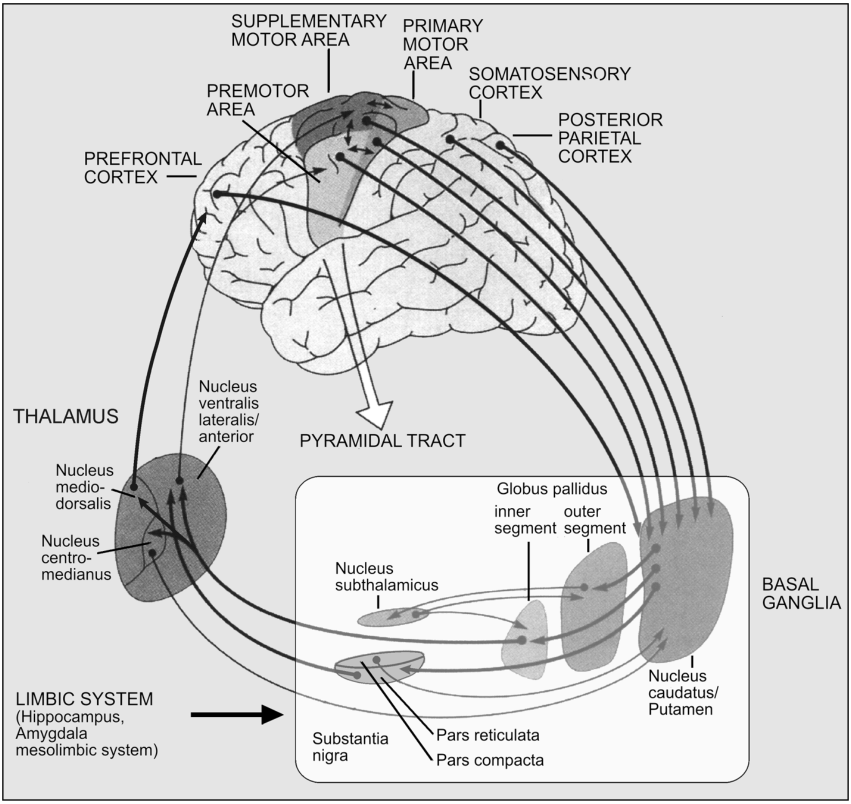


Fig. 3: Control of voluntary actions. The corticostriate tracts run from various cortical areas to the dorsal basal ganglia and from there to thalamic relay nuclei and finally back to the prefrontal, motor, premotor and supplementary motor cortex. The motor and premotor cortex give rise to the pyramidal tract extending to motor circuits in the spinal cord, which control limb muscles. Actions, which are consciously planned in the prefrontal cortex, are executed via the pyramidal tract only after they have passed the "loop" between cortex, basal ganglia and thalamus, and the basal ganglia have "agreed" to the execution. The basal ganglia in turn are under control of limbic centers. For further details see text. (From Roth, 2007).

the limbic system regarding the question, whether these conscious intentions should be realized *here* and *now* and in *precisely that manner*. This guarantees that everything we do is done in the light of past experience laid down in the unconscious emotional and action memory.

6. Summary and Concluding Remarks

We have seen that our actions are controlled by different brain systems in a conscious or unconscious, deliberate or automatic, experience-dependent or inborn-reflex-like manner. Most of what we do in our daily life is done either unconsciously or with only accompanying consciousness. The reason for these differences is that the brain acts in a highly economical way, i.e., whenever possible things are done in a "cheap", fast and precise manner by unconscious subcortical mechanisms, which are either inborn or automatic. Only those types of information and problems that are sufficiently important and for which the brain has no pre-established program, are "uploaded" into cortical consciousness. This system is metabolically expensive, slow, error-prone, but it is the only cerebral system that can handle detailed and complex, often multisensory information and create novel solutions.
Consciousness, without any doubt, is not unique to humans, but found at least in all mammals and birds and maybe in many other animals, although probably not in all forms found in humans (Roth and Dicke, 2005). Since humans, more than any other animals, live in a complex and unstable natural and social environment, consciousness and conscious, voluntary control of actions has become especially important, but nevertheless remains in the hands of the unconscious.

References

Aggleton, J.P. (2000). The Amygdala. A functional analysis. Second edition. Oxford University Press.

Aggleton, J.P. & Brown, M.W. (2006). Interleaving brain systems for episodic and recognition memory. Trends in Cognitive Sciences, 10, 455-463.

Anderson, S.W., Bechara, A., Damasio, H., Tranel D. & Damasio A. R. (1999). Impairment of social and moral behavior related to early damage in human prefrontal cortex. Nature Neuroscience, 2, 1032-1037.

Badre, D. (2008). Cognitive control, hierarchy, and the rostro-caudal organization of the frontal lobes. Trends in Cognitive Sciences, 12, 193-200.

Berridge, K.C. (2007). The debate over dopamine's role in reward: the case for incentive salience. Psychopharmacology (Berl.), 191, 391-431.

Botvinick, M. M. (2004). Hierarchical models of behavior and prefrontal function. Trends in Cognitive Sciences, 12, 201-208.

Botvinick, M. M., Cohen, J. D. & Carter, S. C. (2004). Conflict monitoring and anterior cingulate cortex: an update. Trends in Cognitive Sciences, 8, 539-546.

Clore, G. L. & Huntsinger, J. R. (2007). How emotions inform judgment and regulate thought. Trends in Cognitive Sciences, 11, 393-399.

Coccaro, E. F., McCloskey, M. S., Fitzgerald, D. A. & Phan, K. L. (2007). Amygdala and orbitofrontal reactivity to social threat in individuals with impulsive aggression. Biological Psychiatry, 62, 168-178.

Creutzfeldt, O.D. (1983). Cortex Cerebri. Leistung, strukturelle und funktionelle Organisation der Hirnrinde. Springer, Berlin u.a.

Crick, F. H. C. & Koch, C. (2003). A framework for consciousness. Nature Neuroscience, 6, 119-126.

DeBello, W. M. (2008). Micro-rewiring as a substrate for learning. Trends in Neurosciences, 31, 577-584.

Dolan, R. J. (2000). Functional neuroimaging on the human amygdala during emotional processing and learning. In J.P. Aggleton (Eds.), The Amygdala (2nd edition, pp. 631-653). A Functional Analysis. New York, Oxford: Oxford University Press.

Eccles, J. C. (1982). The initiation of voluntary movements by the supplementary motor area. Arch. Psychiatr. Nervenkr., 231, 423-441.

Fuster, J. M. (2002). Frontal lobe and cognitive development. J. Neurocytol., 31, 373-385.

Goto, Y. & Grace, A. A. (2008). Limbic and cortical information processing in the nucleus accumbens. Trends in Neurosciences, 31, 552-558.

Grace, A. A., Floresco, S. B., Goto, Y. & Lodge, D. L. (2007). Regulation of firing of dopaminergic neurons and control of goal-directed behaviors. Trends in Neurosciences, 30, 220-227.

Graybiel, A.M., Aosaki, T., Flaherty, A.W. & Kimura, M. (1994). The basal ganglia and adaptive motor control. Science, 265, 1826-1831.

Grillner, S., Hellgren, J., Ménard, A., Saitoh, K. & Wikström, M. A. (2005). Mechanisms for selection of basic motor programs – roles for the striatum and pallidum. Trends in Neurosciences, 28, 364-370.

Haggard, P. (2005). Conscious intention and motor cognition. Trends in Cognitive Sciences, 9, 290-295.

Haggard, P., Clark, S. & Kalogeras, J. (2002). Voluntary action and conscious awareness. Nature Neuroscience, 4, 382-385.

Hornak, J., Bramham, J., Rolls, E. T., Morris, R. G., O'Doherty, J. Bullock, P. R. & Polkey, C. E. (2003). Changes in emotion after circumscribed surgical lesions of the orbitofrontal and cingulate cortices. Brain, 126, 1691-1712.

Husain, M. & Nachev, P. (2007). Space and the parietal cortex. Trends in Cognitive Sciences, 11, 30-36.

Jeannerod, M. (1997). The Cognitive Neuroscience of Action. Blackwell, Oxford.

Kolb, B. & Wishaw, I. Q. (1993). Fundamentals of Neuropsychology. New York: Academic Press.

Krakauer, J. W. & Shadmehr, R. (2006). Consolidation of motor memory. Trends in Neurosciences, 29, 58-64.

Kumaran, D. & Maguire, E. A. (2009). Novelty signals: a window into hippocampal information processing. Trends in Cognitive Sciences, 13, 47-54.

LeDoux, J. (1996). The Emotional Brain. New York: Simon and Schuster.

LeDoux, J. (2000). Emotion circuits in the brain. Annu. Rev. Neurosci., 23, 155-184.

Magistretti, P.J. (1999). Brain energy metabolism. In M.J. Zigmond, F.E. Bloom, S.C. Landis, J.L. Roberts & L.R. Squire (Eds.), Fundamental Neuroscience (pp. 389-413). San Diego u.a.: Academic Press.

Magistretti, P.J., Pellerin, L., Rothman, D. L. & Shulman, R. G. (1999). Energy on demand. Science, 283, 496-497.

McHaffie, J. G., Stanford, T. R., Stein, B. E., Véronique Coizet, V. & Redgrave, P. (2005). Subcortical loops through the basal ganglia. Trends in Neurosciences, 28, 401-407.

Mayes, A., Montaldi, D. & Migo, E. (2007). Associative memory and the medial temporal lobes. Trends in Cognitive Sciences, 11, 126-136.

McNab, F., Klingberg, T. (2008). Prefrontal cortex and basal ganglia control access to working memory. Nature Neuroscience, 11, 103-107.

Nieuwenhuys, R., Voogd, J. & van Huijzen, Chr. (1988). The Human Central Nervous System. Berlin, Heidelberg, New York: Springer-Verlag.

Panksepp, J. (1998). Affective Neuroscience. The Foundations of Human and Animal Emotions. New York, Oxford: Oxford University Press.

Passingham, R. (1993). The Frontal Lobes and Voluntary Action. Oxford, New York, Tokyo: Oxford University Press.

Petrides, M. & Pandya, D. N. (1999). Dorsolateral prefrontal cortex: comparative cytoarchitectonic analysis in the human and the macaque brain and cortico-cortical connection patterns. Europ. J. Neuroscience, 11, 1011-1036.

Raine, A., Buchsbaum, M. & Lacasse, L. (1997). Brain abnormalities in murderers indicated by positron emission tomography. Biological Psychiatry, 42, 495-508.

Rolls, E. T. (1999). The Brain and Emotion. New York, Oxford: Oxford University Press.

Roth, G. (2000). The evolution and ontogeny of consciousness. In T. Metzinger (Ed.), Neural Correlates of Consciousness (pp. 77-97). London: Bradford Book, MIT Press, Cambridge, Mass.

Roth, G. (2003). Fühlen, Denken, Handeln. Wie das Gehirn unser Verhalten steuert. Frankfurt: Suhrkamp-Verlag.

Roth, G. (2007). Persönlichkeit, Entscheidung und Verhalten. Stuttgart: Klett-Cotta.

Roth, G. & Dicke, U. (2005). Evolution of the brain and intelligence. Trends in Cognitive Sciences, 9, 250-257.

Rushworth, M. F. S. & Behrens, T. E. J. (2008). Choice, uncertainty and value in prefrontal and cingulate cortex. Nature Neuroscience, 11, 388-397.

Samson, R. S. & Paré, D. (2005). Activity-Dependent Synaptic Plasticity in the Central Nucleus of the Amygdala. Journal of Neuroscience, 25, 1847-1855.

Schultz, W. (2007). Behavioral dopamine signals. Trends in Neurosciences, 30, 203-210.

Seth, A. K., Dienes, Z., Cleeremans, A., Overgaard, M. & Pessoa, L. (2008). Measuring consciousness: relating behavioural and neurophysiological approaches. Trends in Cognitive Sciences, 12, 314-321.

Smythies, J. (1997). The functional neuroanatomy of awareness: With a focus on the role of various anatomical systems in the control of intermodal attention. Consciousness and Cognition, 6, 455-481.

Squire, L. R. (1987). Memory and Brain. New York: Oxford University Press.

Swanson, L.W. & Petrovitch, G. D. (1998). What is the amygdala? Trends in Neurosciences, 21, 323-331.

Tsuchiya, N. & Adolphs, R. (2007). Emotion and consciousness. Trends in Cognitive Sciences, 11 (4), 158-167.

Tulving, E. & Markowitsch, H.J. (1998). Episodic and declarative memory: Role of the hippocampus. Hippocampus, 8, 198-204.

Uddin, L. Q., Iacoboni, M., Lange, C. & Keenan, J. P. (2007). The self and social cognition: the role of cortical midline structures and mirror neurons. Trends in Cognitive Sciences, 11, 153-157.

Ullsperger, M. & von Cramon, D. Y. (2003). Error Monitoring Using External Feedback: Specific Roles of the Habenular Complex, the Reward System, and the Cingulate Motor Area Revealed by Functional Magnetic Resonance Imaging. Journal of Neuroscience, 23, 4308-4314.

Wiech, K., Ploner, M. & Tracey, I. (2008). Neurocognitive aspects of pain perception. Trends in Cognitive Sciences, 12, 306-313.