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Advances and Technical Standards in Neurosurgery

Volume 37

SpringerWienNewYork

SpringerWienNewYork

Sponsored by the
European Association of Neurosurgical Societies

Advances and Technical Standards in Neurosurgery

Vol. 37

Edited by
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SpringerWienNewYork

Printed in Austria

SpringerWienNewYork is part of Springer Science Business Media
springer.at

Typesetting: Thomson Press (India) Ltd., Chennai
Printing: Holzhausen Druck GmbH, 1140 Wien, Austria

Printed on acid-free and chlorine-free bleached paper
SPIN: 80032610

With 47 (partly coloured) Figures

Library of Congress Control Number: 2011931979

ISSN 0095-4829
ISBN 978-3-7091-0672-3 SpringerWienNewYork

Preface

Advances and Technical Standards in Neurosurgery was conceived in 1972 by its founding fathers Jean Brihaye, Bernard Pertuiset, Fritz Loew and Hugo Krayenbühl at a combined meeting of the Italian and German Neurosurgical Societies in Taormina. It was designed to complement the European post-graduate training system for young neurosurgeons and was first published in 1974 initially through sponsorship by the European Association of Neurosurgical Societies. Subsequently adopted by Springer-Verlag, the Publishers, its circulation has benefited considerably from inclusion in Springer e-book series.

All contributions have been published in English to facilitate international understanding.

The ambition of all successive editorial boards has been to provide an opportunity for mature scholarship and reflection, not constrained by artificial limits on space. The series provides a remarkable account of progress over the past 37 years, both with regard to advances, detailed descriptions of standard operative procedures and in-depth reviews of established knowledge. The present volume should appeal to both experienced neurosurgeons and young neurosurgeons in training alike.

The Editors

Contents

Advances

The neuroscientific foundations of free will. Z. H. RAPPAPORT, Department of Neurosurgery, Rabin Medical Center, Petah-Tiqva and Sackler School of Medicine, Tel-Aviv University, Tel-Aviv, Israel

Functional exploration for neuropathic pain. J. MAARRAWI[1,2], P. MERTENS[2,3], R. PEYRON[2,4], L. GARCIA-LARREA[2], and M. SINDOU[3], [1]St Joseph University (Faculty of Medicine) and Hôtel-Dieu de France Hospital (Department of Neurosurgery), Beirut, Lebanon, [2]INSERM U 879 (Central Integration of Pain), Lyon and St-Etienne, France, [3]Functional Neurosurgery Department, Hôpital Neurologique, HCL, Lyon, France, [4]Neurology Department, Hôpital Bellevue, St-Etienne, France

Experimental reconstruction of the injured spinal cord. A. Hejčl[1,2,3], P. Jendelová[1,2], E. Syková[1,2], [1]Institute of Experimental Medicine, Academy of Sciences of the Czech Republic, Prague, Czech Republic, [2]Department of Neuroscience and Center for Cell Therapy and Tissue Repair, 2nd Faculty of Medicine, Charles University, Prague, Czech Republic, [3]Department of Neurosurgery, Purkinje University, Masaryk Hospital, Usti nad Labem, Czech Republic

Technical standards

Myelomeningocele (open spina bifida) – surgical management. N. AKALAN, Department of Neurosurgery, Hacettepe University School of Medicine, Ankara, Turkey

Chiari type I malformation in children. L. MASSIMI, F. NOVEGNO, and C. DI ROCCO, Pediatric Neurosurgery, Catholic University Medical School, Rome, Italy

Treatment of infections of the spine. M. STOFFEL, C. STÜER, F. RINGEL, and B. MEYER, Department of Neurosurgery, Klinikum rechts der Isar, Technische Universität München, Munich, Germany

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Advances

The neuroscientific foundations of free will

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With 2 Figures

Contents

Abstract

The issue of free will is at the heart of understanding ourselves, what it means to be a conscious, thinking, and responsibly acting human being. A position on this issue has profound implications on how we see ourselves as moral agents and on our place in the universe. The developments in neuroscience over the last half century have provided us with much data concerning the function of the brain and its relationship to the mind. In this article we shall review contributions of both neurosurgeons and other neuroscientists to our understanding of free will. The volitional motor model will be emphasized for heuristic purposes. Ultimately, by understanding the limits of our freedom, we can enhance our concept of the meaning of our lives.

Keywords: Free will; neuroscience.

We all have an authentic and immediate belief that we are in control over our actions. This belief has been discussed over the millennia in three spheres of thought: Religion (omnipotent and omniscient divinity), ethics (responsibility for actions), and science (the mind and physical causes).

The issue of free will is at the heart of understanding ourselves, what it means to be a conscious, thinking, and responsibly acting human being. A position on this issue has profound implications on how we see ourselves as moral agents and on our place in the universe.

The developments in neuroscience over the last half century have provided us with much data concerning the function of the brain and its relationship to the mind. Neurosurgeons have been an important part in furthering our knowledge of brain function both in health and disease. In this article we shall review contributions of both neurosurgeons and other neuroscientists to our understanding of free will. Ultimately, by understanding the limits of our freedom, we can enhance our concept of the meaning of our lives.

Philosophical introduction, the free will debate

Free will requires forking paths into the future, with the power to go down one of the paths rather than the other. We strongly have the feeling that we have the capacity to freely choose between different possibilities of action. The thesis that we have free will is called libertarianism. There is, however, a conceptual problem in believing in a free will generator in our brains. Science posits a cause of behavior. We feel we are free to choose our next act, which is therefore unpredictable. Since the behavior is not random it must have a cause. If behavior has a cause it is not free. If the brain's free thought module creates actions out of past experiences and memories it is deterministic. If it is not responsive to past experiences it becomes random, which is a far cry from responsible free will. As William James wrote:

> "*If a free act be a sheer novelty, that comes not from me, the previous me, but ex nihilo, and simply tacks itself on me, how can I, the previous I, be responsible? How can I have any permanent character that will stand long enough for praise or blame to be awarded?*" [40].

In contrast, determinism implies that one's past allows only one possible path for the future. The world is governed by laws of physics. I cannot originate actions that are not already predetermined by my prior state. The classical argument for determinism was provided by "Laplace's Devil":

> "*An intelligence which in a singular instant could know of all the forces which animate the natural world, and the respective situations of all the beings that made it up, could, provided it was vast enough to make an analysis of all the data so supplied, be able to*

> *produce a single formula which specified all the movements in the universe from those of the largest bodies in the universe to those of the lightest atom*" [47].

If a supercomputer could know the positions of all the energy particles in the universe and their interactions, it should be able to predict the next events. Such global knowledge is of course impossible. Complex systems, such as the brain, have too many variables to be presently fully describable except in statistical models using methods such as chaos theory. However, for all practical purposes, the scientific method posits a deterministic cause for every effect. Some scientists have attempted to link the indeterminacy of quantum mechanics with the possibility of free will [13]. For example, Roger Penrose posits that the mind can perform non-computable operations that have their source in quantum gravity, a speculative theory bridging the gap between classical and quantum mechanics [64]. Hameroff and Penrose [36] proposed the microtubules of the neuronal cell's cytoskeleton as the site where quantum mechanics works its magic, allowing for the undetermined will to arise. However, this argument contains a logical flaw. Will that arises from a random quantum generator can hardly be equated with the libertarian's notion of free will. How free would we be if our choices are simply determined by a quantum coin flip? In any event quantum mechanics applies only to subatomic scale. At the size of even intraneural microtubules and at ambient temperatures only the classical physics of determinism applies.

Compatibilism allows for the coexistence of determinism with a soft form of free will, especially as it relates to moral issues. Enunciated most forcefully by David Hume in the 18th century, he points out that determinism does not exclude meaningful free will; what matters is that individuals' choices are the results of their own desires and preferences, and are not overridden by some external (or internal) force:

> "*By liberty, then, we can only mean a power of acting or not acting according to the determinations of the will; that is, if we choose to remain at rest, we may; if we choose to move, we also may. Now this hypothetical liberty is universally allowed to belong to everyone who is not a prisoner and in chains*" [38].

Espoused also by Thomas Hobbes in the 17th century and John Stuart Mill in the 19th century, classical compatibilism was popular amongst most philosophers dealing with issue of free will, and for good reason: one could hold a determinist view-point of the universe, not have to invoke mind-body dualism, and yet maintain a form of freedom of action compatible with our moral sense of personal responsibility. Causality does not necessarily imply coercion.

It has been commonly supposed that this sophisticated approach, favored by most philosophers today, was at odds with people's everyday intuition in favor of a robust form of indeterministic free will. If I wiggle my fingers at random, this act is completely unpredictable and subject to my will alone.

However, when tested in an experimental setting, it appears that a large proportion of everyday subjects are comfortable with maintaining the compatibilist notion of free will despite being presented with a completely deterministic frame of reference, as long as they are faced with a concrete situation [60]. For example, in one scenario, a world is posited in which a Laplacian supercomputer can predict future human behavior based on its knowledge of all laws of nature. In this hypothetical world an individual robs a bank, an action that could be predicted by the computer. Most study participants still felt that the bank robber was morally culpable, a view that fits with a compatibilist approach. Yet when presented with an abstract question as to what our universe is like, people from all cultures, both east and west, will come down on the side of free will in an indeterministic universe [67].

It is therefore not surprising that observations in clinical neurosciences have had an unsettling effect on the public at large when it comes to an understanding of self, consciousness, and free will. In the following section I shall outline some of the observations from neurosurgical patients, neurophenomenology following brain injury, and from neuropsychological experiments that are germane to the issue of free will. I shall argue that these observations present a paradigm shift in the understanding of ourselves that is gradually impacting society at large.

The neurophysiology of free will

Brain activation precedes movement decision

In one of the most widely cited neurophysiologic studies on volition, Libet et al. [50] demonstrated that the brain initiates a movement before the experimental subjects becomes aware of wanting to perform it. In the study the test person was seated in front of a clock the second hand of which revolves at a speed of 2.56 sec/revolution. He was instructed to bend his finger whenever he wanted to and to report where the second hand was positioned when first becoming aware of his will to move. He was also to note the time when becoming aware of actually moving. EEG and EMG recordings were performed. A movement-related readiness potential [44], originating from the supplementary motor area (SMA), was observed on the EEG tracing about 0.5–1 sec before prior to the action and about 0.2 sec before becoming aware of wanting to move his finger. The subject also thought that he had begun moving his finger on the average of 86 msec before he actually did (Fig. 1). The authors' conclusion was

> "*that cerebral initiation of a spontaneous, freely voluntary act can begin unconsciously, that is, before there is any (at least recallable) subjective awareness that a 'decision' to act has already been initiated cerebrally*" [50].

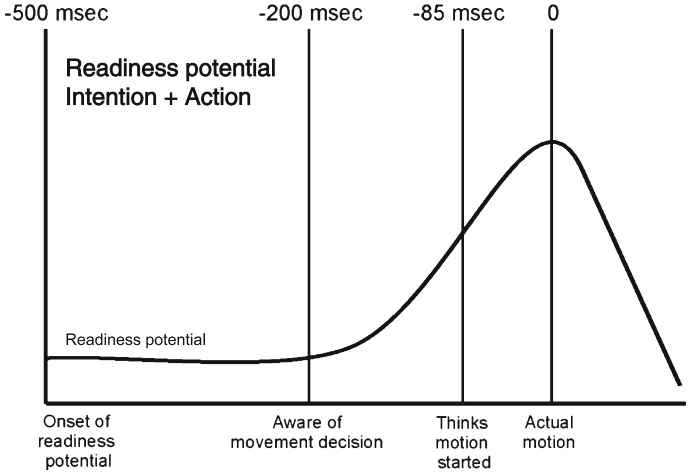

Fig. 1. The readiness potential and its relation to intention and action. The readiness potential arises between 1 and half a second prior to the onset of action. The subject becomes aware of his intention to move 200 msec before the action. He thinks that he has started to move about 85 msec before the movement

Libet himself felt uncomfortable with the study's implication that free will might have been negated. He proposed that free will could still act by vetoing the finger's movement after the subject had become aware of his intention [51]. However the "free won't" could also have a similar subconscious mechanism with an associated readiness potential [62]. In a study by Kühn and Brass [46] experimental subjects were asked to respond to a "go" signal and their reaction time was measured. Randomly interspersed were "stop" and "decide" signals, where the subjects could either veto their ongoing action or decide what to do. When subjects were in the "decide" mode, their reaction time was significantly slower than in spontaneous mode, allowing the experimenter to identify it. When interviewed, the participants were not able to distinguish between spontaneous and deliberative vetoes. The authors interpret this as showing that "free wont" is similar to "free will": a retrospective construction of the either positive or negative action that was initiated before conscious awareness.

Libet's results, while being subjected to a number of criticisms [55], have been replicated several times [48, 70] and have been elaborated upon. Haggard and Eimer [33] asked experimental subjects to freely move either their left or right hand. A lateralization of the readiness potential was observed contralateral to the hand moved. This occurred long before the experimental subject became aware of his will to move and allowed prediction of the side of the motion. Therefore, movement selection also precedes awareness.

In order to overcome the methodological problems inherent in Libet's experiment (self-reported timing and subjective memory), Matsuhashi and

Hallett [54] attempted to minimize the dependency on subjective recall when exploring the relationship between intention and movement genesis. The subjects were asked to perform self-paced finger movements with explicit directions to react to their feeling of intention to move as quickly as possible. Intermittent stop tones were sounded randomly throughout the task. When the subject had no intention to move at the time, he was to ignore the tone. If he had already decided to move, the subject was to stop his movement upon hearing the tone while noting his awareness of the intention. The timings of tones and movements were all recorded and the distribution of relative times between movements and tones was graphed. Tones that actually vetoed movements did not contribute to the plot. An analysis of the results showed that the time of conscious intention to move occurred too late to be the cause of movement genesis as measured by the readiness potential, thereby confirming Libet's results. Both the feeling of intention and the movement are results of unconscious processing.

In a recent functional magnetic resonance imaging (fMRI) study, brain activity in the prefrontal and parietal areas preceded the awareness of wanting to move by a full 10 sec [72]. Subjects were asked to relax and look upon a stream of letters on a screen. They were to press one of two buttons next to their left or right index fingers whenever they felt the urge and to remember the letter on the screen when their motor decision was made. fMRI images were analyzed and correlated with the freely generated movements. Predictably the contralateral primary motor cortex and the SMA encoded the subjects' motor decision during the execution of the movement. More interestingly, two brain regions encoded with high accuracy whether the subject was about to choose the left or right response up to10 sec prior to the conscious decision. These areas were within the frontopolar cortex and in the parietal cortex (stretching from precuneus to posterior cingulate). The data suggests

> "*a tentative causal model of information flow, where the earliest unconscious precursors of the motor decision originated in the frontopolar cortex, from where they influenced the buildup of decision-related information in the precuneus and later in SMA, where it remained unconscious for up to a few seconds*" [72].

Biasing freely willed decisions

An important point of contention in the free will debate is in the genesis of spontaneous freely willed actions. We are rather oblivious of potential triggers to our actions, tending to attribute them to spontaneity or reasoning.

Taylor and McCloskey [75] studied the effect of a hidden stimulus on voluntary movements. A small stimulus was masked by a large stimulus presented 50 msec later by inhibition of cortical processing. These stimuli were presented in two visual locations related to different movements. Despite not being able to perceive the smaller stimulus, subjects executed the appropriate motor response for each stimulus. The authors concluded that separate programs for motor movement can be stored for subsequent use and can be triggered without the need for subjective awareness of the stimulus.

An outside trigger to movement can also be manipulated in such a way that the experimental subject is deluded into thinking that he himself initiated the action. Subjects were asked to move their right or left hand randomly on hearing the click of a transcranial magnetic stimulator (TMS) placed over their motor cortex. Stimulation caused a preference for contralateral hand movements at short response times. The participants thought that they had willed the response [10], unaware that it had actually been caused by the TMS.

The perceived onset of motor intention can also be shifted backward in time by TMS stimulation of the presupplementary motor area while shifting the perceived time of action execution forward in time [49]. The size of the effect was similar regardless of whether TMS was applied immediately after the action or 200 msec later. The authors conclude that the perceived onset of intention depends, at least in part, on neural activity that takes place after the execution of action. These results imply that our experience of intention are not fully formed prior to the action but are also dependent on neural activity after the event.

The feeling of agency (I am the one who's doing it)

We normally feel in that we are causing and controlling our own actions. In some pathological disorders, such as schizophrenia, impairment of agency have been attributed the inability to predict the outcome of their actions due to misinterpretation of their sensory results [52]. In alien hand syndrome there is a disconnection between the cerebral motor planning system and the primary motor cortex [1]. The patient's affected hand has a life of its own, performing actions not under the voluntary control of the owner. While appropriately responding to external cues, the hand movement is not willed by the patient. For example, a patient reaches for a cup with his uncontrolled arm despite having just declared that he would let the drink cool before drinking it [23]. While patients clearly identify that they are connected to the involuntary movement, they do not identify with being the source of the movement, therefore lacking the feeling of agency necessary for ownership of the movement [53]. This syndrome is caused by lesions in the corpus callosum, also involving the mesial frontal lobe, with some variants of the syndrome being be due to parietal lobe injuries [68].

There are a number of other clinical conditions were the perception of action is distorted. Patients with tics are unable to feel whether the movements are voluntary or not. If pressed, they will opt for voluntary motion [35]. After amputations patients may develop a sensation of moving their phantom limb:

> *I placed a coffee cup in front of John and asked him to grab it [with his phantom limb]. Just as he was reaching out, I yanked the cup away.*
> *'Ow', he yelled, 'don't do that'!*
> *'What's the matter?'*
> *'Don't do that', he repeated, 'I had just gotten my fingers around the cup handle when you pulled it. That really hurts!'* [65].

In anosognosia, often seen following central non-dominant hemisphere strokes, patients believe that they are making movements when none occur [6]. Posterior insular damage can also alter the phenomenology, but based on a different pathophysiology [42]. The insula, which receives sensory input from different parts of the body [16], may be instrumental in the construction of a feeling of self and of the feeling of ownership of the body in motion [20, 77]. What is common to all of these pathological conditions is that there is a mismatch between perceived volition and actual movement.

For a person to think that an action was willed by himself there are three requirements: consistency, priority, and exclusivity [83]. The thought should be consistent with action, the thought should immediately precede the action, and it should not be accompanied by other potential causes.

A well-known example of the absence of consistency is the electrical stimulatory exploration of the brain surface by Wilder Penfield during awake surgery for the treatment of epilepsy [63]. Motor cortex stimulation would cause the hand of the patient to move. Patients would respond: "*I didn't do that, you did*". The patients did not feel that their actions were consciously willed as there was no thought process preceding them.

In fact, most of our actions in daily life are automatic and related to external or internal stimuli. We swat a mosquito as a reflex action without deliberation. We catch ourselves scratching the mosquito bite and only then begin to deliberate when to stop. Willed actions are a relatively minor part of our daily movement portfolio [4].

We ascribe actions to our will when they appear in temporal proximity after our thoughts about them (priority). Wegner and Wheatley [82] explored the time frame involved in an experimental setting. Two subjects were simultaneously holding a computer mouse with which they could move a cursor on a screen. The experimental subject heard words describing some of the 50 objects on the screen during a 30 sec period, after which they were to stop the cursor together. Unbeknownst to the subject the second person was a collaborator of the experiment and received instructions about when and where to stop the cursor. If the priming word occurred between 1 and 5 sec before the stop, the subject believed more strongly that he had intentionally stopped the cursor by himself. The subjects were led to experience a causal link between a thought and an action, the feeling that they willfully performed an action, which, however was actually performed by someone else. We can conclude from this study that our brain interprets our actions from a cause and effect point of view. We are not aware of the underlying machinery causing our actions and can be manipulated into attributing others' actions as our own. The will is not a psychological force that causes action. Rather, it is a conscious experience interpreting a causal relationship between cognition and action.

The third component of agency is exclusivity. If alternative external causes can be attributed to the performed action, the sense of authorship is undermined. In Milgram's famous experiment on obedience in Yale University psychology undergraduate students, participants agreed to give extremely painful electrical shocks to fellow students (actually actors) in order to comply with the requirements of the experiment [57]. As a possible explanation of the students' behavior, Milgram proposed that

> "*the essence of obedience consists in the fact that a person comes to view himself as the instrument for carrying out another person' s wishes, and he therefore no longer sees himself as responsible for his actions*".

Similarly in hypnosis actions performed by the subject are perceived as involuntary and are ascribed to the hypnotist [84]. On the other hand if an outside causal mechanism is not perceived, people will be deluded into thinking that they willed the action, as showed in the TMS experiment of Brasil-Neto et al. [10].

The neuroanatomical nuances of agency have been investigated by Farrer et al. [26]. The authors modulated the feeling of agency in volunteers by asking them to control the movements of a virtual hand. There were four experimental situations: (1) the subject had full control over the virtual hand; (2) the virtual hand appeared rotated by 25° with respect to movements made by the subject; (3) the movements of the virtual hand appeared rotated by 50°; and (4) where the movements of the virtual hand were controlled by another person and did not correspond to the hand movements of the subject. The experiment was performed while the subjects were undergoing positron emission tomography (PET). As the discrepancy between the hand movement of the subject and the virtual hand grew, the right inferior parietal lobe became accentuated on the PET scan and the accentuation of the right posterior insula declined. Lesions of the posterior right parietal lobe have been seen in alien hand syndrome and in cases of severe neglect [8, 21]. Insular activity tends to maximize when there is congruence between action and outcome [27]. The interplay between these two regions forms part of the substrate of our sense of agency.

The neuroanatomical substrate of free will

The quest for the location of free will in the brain is reminiscent of the attempt of philosophers to pinpoint the abode of the soul within the human body. While the heart was a favorite container for many, René Descartes, the champion of mind-body duality, placed the seat of the soul in the pineal gland:

> "*My view is that this gland is the principal seat of the soul, and the place in which all our thoughts are formed. The reason I believe this is that I cannot find any part of the brain, except this, which is not double. Since we see only one thing with two eyes, and hear only one voice with two ears, and in short have never more than one thought at a time, it must necessarily be the case that the impressions which enter by the two eyes or by the two ears, and so on, unite with each other in some part of the body before being considered by the soul. Now it is impossible to find any such place in the whole head except this gland; moreover it is situated in the most suitable possible place for this purpose, in the middle of all the concavities; and it is supported and surrounded by the little branches of the carotid arteries which bring the spirits into the brain*" [15].

Damasio and Van Heusen [18] reported a case of a kinetic mutism in a young woman with anterior cingulate damage. She would not speak spontaneously, but was, however, able to repeat words slowly. Following her recovery she reported that she could follow conversations but did not speak because she had nothing to say. Her mind was empty. Francis Crick [17] on hearing of this case suggested that the seat of will had been discovered.

The view that we can find a single locus in the brain as the source for complex behavior is too simplistic. The brain is organized as a massive parallel processor with feedback loops that can be described in terms of dynamical system theory [69]. Gazzaniga and Sperry, in their studies on patients after corpus callosotomy (split brain) surgery for epilepsy, have shown that there is no holistic center as the locus of an individual's mental capacity [29]. Corpus callosotomy accomplishes a disconnection between the two hemispheres of the brain. Its therapeutic purpose is to stop the propagation of epileptogenic electrical impulses form one side of the brain to the other. As a result, however, the functional communication between the two hemispheres is also curtailed. These patients have two largely separate mental systems, each with its own interpretation of the environment. There are two systems of will in the same patient, each hemisphere giving differing views about life goals and opinions. Patients may also display conflicting wills: the right hand pulling one's pants up while the left one tries to pull them down. The left hemisphere, containing the language capacity, acts as a confabulator. It provides for a plausible story that explains the otherwise strange actions of the disconnected right hemisphere. We can conclude from the results in split-brain patients that reasoning, will, and the generation of actions can be fractured and compartmentalized into different brain regions. Our sense of conscious choice may produce interpretation of our actions that are not factually correct so as to preserve the illusion of control with the left hemisphere containing an "interpreter module".

Confabulation is present in a variety of clinical neuropathological conditions such as Alzheimer's disease, schizophrenia, Anton's syndrome, Capgras' syndrome, and Korsakoff's syndrome [37]. As in split-brain syndrome, confabulation can also arise in cognitively intact patients when their output does not match their internal thinking process. Delgado, one of the pioneers of electrical stimulation of the brain, described a patient whose anterior internal capsule was stimulated, causing him slowly turn his head and body. When asked what he was doing, the patient confabulated: "*I am looking for my slippers; I was looking under the bed*" [22]. The patient felt that he was in charge of his actions and had to find a reason to make them seem plausible. Yet there was clearly a lack of connection between the brain source of action and his presumed will.

Electrical stimulation of the brain has provided a fruitful model for the exploration of will. The conscious patient can verbally communicate while specific anatomical sites of his brain are activated. Kremer et al. [45] performed an exploratory electroencephalographic recording and electrical stimulation session in a patient with intractable epilepsy. When stimulating the ventral bank of the anterior cingulate sulcus, the patient felt an irresistible urge to grasp. The patient gave into the urge, looked around for an appropriate object, and grasped it. The anterior cingulate gyrus lies at the interface between frontal cortex and motor centers and, in its ventral part, is part of the limbic system connected with emotions and motivations [9]. It may be said to play a role in the aspect of volition called striving.

The prefrontal cortex is the hallmark of the evolutionary development of the brain in the human and intimately involved in higher cognitive function. The dorso-lateral prefrontal subcortical circuit organizes information to facilitate action (working memory), while the orbitofrontal circuit allows the integration of limbic and emotional input into behavioral responses [7]. Specifically the dorsolateral prefrontal cortex (DLPFC) has been related to volition. When damaged, stereotypical responses to the environment such as repeatedly putting on ones glasses or eating whatever food place on ones plate, have been observed [73]. The DLPFC is activated on fMRI studies of willed, self-generated actions [39], while when actions are spontaneous, only more posterior frontal lobe areas, such as the supplementary motor area (SMA) together with postrolandic, cerebellar and basal ganglia areas are active. Hyder et al. [39] point out that the site of activation in the DLPFC varies between different modalities of willed action, such as motion versus speech. We are therefore not speaking of a "will center", but rather of an area involved in aware action planning with differing location within the DLPFC according to type. Stephan et al. [74]

investigated the fMRI pattern in finger tapping tasks requiring different degrees of conscious intervention. Only in situations requiring fully conscious adaption were DLPFC and anterior cingulate prominent. They concluded that the DPFLC is involved in fully conscious motor control which includes motor planning.

Electrical stimulation of the SMA in the conscious patient during epilepsy surgery has also produced involuntary motor responses [28]. Patients reported the urge to move a body part or that they were about to move it. Stronger stimulation actually caused complex movements. Bilateral movement could be produced by right-sided SMA stimulation, but not by left-sided stimulation. The SMA together with the pre-SMA and more lateral premotor areas is largely the source of the readiness potential. The SMA has been implicated in the planning of the sequence of movements from memory rather than from visual clues and in bimanual tasks. Its relative role to the pre-SMA is still under investigation [59].

To add to the developing picture is the recent study by Desmurget et al. [25] in which the parietal lobe was electrically stimulated during awake neurosurgery. Patients reported a feeling of wanting to move a specific body part. When the intensity of stimulation was increased, it could produce the illusion that the movement had already been performed, while the patient had in fact remained perfectly still. As mentioned before, patients with ischemic damage to the inferior parietal lobule selectively differ in the temporal judgments of their intentions to move compared with normal controls [70]. The difference in response between electrical stimulation of the SMA and that of the parietal lobe suggests two distinct processes with respect to conscious intention: (1) A conscious correlate of planning motor actions within the SMA/pre-SMA involving the DLPFC; (2) A virtual reality sensory preview of the motor action within the parietal lobe that feeds back to the SMA. This sensory prediction could create the sense of authorship necessary to feel that one owns ones actions [34].

The classical model of choice involves a sequential series of brain activation: from sensory representation of the options through mental/neural processing to reach the decision stage, and finally to motor output [30]. While the EEG and fMRI can locate areas of activity involved in the behavior, their temporal discrimination is poor. Magnetoencephalography can provide better temporal resolution in addition to fairly specific anatomical localization. Using this technique in different choice conditions has shown that brain activation is not sequential, but with multiple recurring activation peaks during the choosing process [32]. In the first stage of activation, primary and associative visual cortices become active reflecting the sensory input and its processing. During the second stage, neural activation peaks occurred in a wide variety of brain regions depending on the choice conditions (DLPFC, memory and cognitive areas). This can be thought of as an option evaluation stage. In the third stage (action planning and intention), activation peaks occurred in the parietal area with a sub-distribution according to the different choice conditions. The parietal area is not only involved with sensory representation of spatial coordinates necessary for action planning, but is responsive to cognitive context as well. SMA activation occurred in all choice conditions during the second and third stages. The final stage consists of the activation of the contralateral sensorimotor cortex corresponding to the execution of the action.

Based upon the extensive experimental work on this subject, of which only highlights have been presented here, we can form a well-grounded dynamic anatomical picture of movement genesis and volition in the brain [35]. Movement planning arises in the pre-SMA and SMA under the influence of prefrontal and limbic structures. The parietal lobe is activated to allow sensory modeling and stays in communication with the mesial motor areas. The primary motor cortex is then activated initiating the movement. Sensory feedback to the parietal lobe allows for the feeling of agency when there is a match between the movement and the volition. Insular activation in parallel to this process is correlated with body image and ownership of the action. Ultimately some of

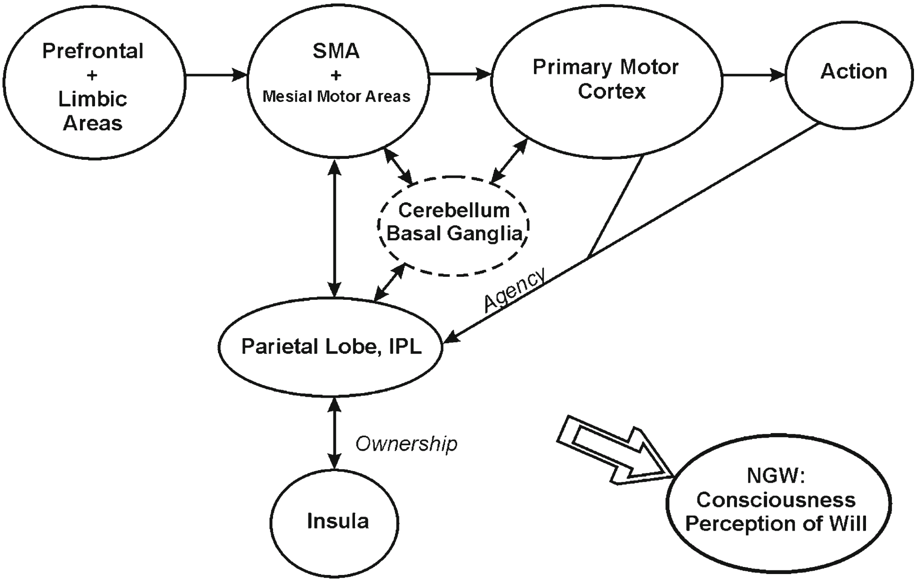

Fig. 2. A neuroanatomical sketch of willed motion: The awareness of agency is subject to the feedback between the actual movement and the sensory model created in the parietal lobe. The sense of body ownership is dependent on insular processing. It must be remembered that activations are dynamic and not sequential as pictured. SMA is the supplementary motor area, IPL the inferior parietal lobule, NGW the neural global workspace