Review Article

Conscious, Unconscious & Involuntary Control of Locomotion & Comparable Stereotyped Motor Behaviors

Pierre A. Guertin*

Dept. of Psychiatry & Neurosciences, Laval University, Canada

ABSTRACT

It is generally believed that voluntary movements are controlled by brain structures. Signals from cortical areas (e.g., primary motor cortex) are specifically considered to underlie the expression of volitional motor behaviors such as pointing finger or hand reaching for a bottle. However, there are also compelling evidence and breakthrough findings demonstrating that some motor behaviors, especially rhythmic and/or stereotyped, can also be unconsciously and/or involuntary controlled for the most part. For instance, the classical Ia reflex, a simple stereotyped, monosynaptic, and involuntary mediated motor response can be consciously felt in some circumstances whereas the Ib disynaptic reflex is always completely involuntary and unconscious. The pioneering work of Graham Brown in the early 1900s provided evidence of involuntary control mechanisms even for more complex stereotyped behaviors such as basic walking or running that can be mediated in complete absence of supraspinal inputs. In the 70s, Grillner and Zangger clearly showed that basic locomotor activities can indeed be induced without brain structures and sensory inputs in completely decerebrate and rhizotomized animals. Other findings showed subsequently comparable brainstem and/or spinal control mechanisms for many other complex rhythmic stereotyped motor behaviors such as mastication, deglutition, respiration, micturition, defecation, and ejaculation. The relevance of such findings for research on the neural control of movements as well as on the role of neural correlates of mindful (e.g., DMN, DAN, etc.) movements is discussed.

Keywords: Consciousness, mindfulness, reflex, walking, motor cortex, brainstem, spinal cord.

Brain centers and voluntary motor control in mammals

It is a general belief that most movements are voluntarily and consciously initiated and, hence, essentially controlled by the brain – mental processes would be at the origin of movements purposefully executed (so-called volitional actions), as proposed by Descartes a few centuries ago (1). A pivotal role for the primary motor cortex in volitional movements has also been proposed by several neuroscientists more recently. Electrical stimulation of the primary motor cortex (i.e., located in the frontal lobe, anterior to the central sulcus) was shown to have the lowest threshold for inducing movements (2) – its activation was reported in cats and dogs to

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*Correspondence: Professor Pierre A. Guertin, Dept. of Psychiatry & Neurosciences, Faculty of Medicine, Laval University, Laval University Medical Center, Quebec City, Quebec, Canada, G1V 4G2. Email: pierre.guertin@crchudequebec.ulaval.ca

trigger per se the expression of specific movements. That led to the notion that the primary motor cortex is the main control center of most movements (3).

In humans, Penfield and Jasper from McGill University were the firsts to report that stimulation of discrete motor cortex areas with an electrode can trigger site-specific, coordinated muscle responses (4) which led to a map of motor cortex functions better known as the motor homunculus. For instance, stimulation of the most caudal area of the motor cortex elicited a contraction of muscles controlling the fingers on the opposite side of the body (contralaterally). That homunculus contributed to show also that motor cortex areas are organized somatotopically in an orderly fashion so that adjacent muscles are controlled by adjacent regions of the primary motor cortex (1). Subsequently, it was shown that other regions of the brain such as the prefrontal cortex, premotor cortex, and supplementary motor cortex play also a significant role in voluntary motor control by planning, controlling, and executing so-called volitional movements (1). However, those breakthrough findings do not necessarily mean that simple or more complex motor behaviors can’t, in turn, be elicited and controlled involuntarily or in a total absence of consciousness.

Does a boundary between conscious and unconscious movements exist?

However, prior to further explore this question, another problem needs imperatively to be addressed. Those two words – consciousness and unconsciousness – have long been a subject of debate primarily for conceptual, metaphysical, philosophical, and semantic reasons. They have a considerably different meaning depending on the situation or the person (5). For some people, consciousness and specifically self-consciousness refer to being shy and worrying about what others think of ourself. In contrast, the *Collins* English dictionary defines consciousness simply as the state of being awake (3). Some researchers such as Dr Uriah Kriegel have proposed that consciousness includes self-consciousness or ‘intransitive self-consciousness’ since the latter can’t be expressed without the former (6).

Descartes had proposed a long time ago that the pineal gland was the center of consciousness and consciously induced actions – i.e., volitional movements (7). Between the intention of moving and its execution, the pineal gland was imagined by Descartes as the ‘central command center’ from where the final decisive signal is sent to each specific muscle for its contraction. Nowadays, physicians use instead more clinically relevant definitions for practical and professional reasons. In some medical areas, consciousness is considered as a level of responsiveness either verbal, motor, or brain activity-related. It is thus perceived as a continuum of states ranging from full alertness and comprehension, through disorientation, delirium, loss of meaningful communication, and finally loss of reflexes (8).

For anesthesiologists, unconsciousness is defined by a loss of alertness or full anesthesia (9) assessed with scales such as the Glasgow Coma Scale (10). All in all, one of the main problems when trying to understand voluntary, conscious, unconscious, reflex, and/or involuntary motor control mechanisms is not of scientific origin – it is instead essentially of conceptual and semantic origin. The word consciousness is ambiguous because it is a word used by everyone but with different meanings and for different purposes (11).

The motor cortex can, in some circumstances, be accessory for the expression of relatively simple motor response

An elegant study by Prof J. Martin in genetically engineered mice showed that corticospinal neurons originating from the primary motor cortex can be 'deleted' without detectable changes on locomotion (12). With the gene EphA4 removed unilaterally from the cerebral cortex, EphA4 KO mice remained capable of well-coordinated walking which, in turn, demonstrated that circuits in other parts of the central nervous system (*e.g*, brainstem and spinal cord), not affected by the gene manipulation, suffice to control conscious or at least volitional walking. In contrast, it has been shown also that nerve impulses from the primary motor cortex can generate movements even if someone is unaware of them.

Indeed, the Alien hand syndrome (AHS) is a rare neurological disorder that leads to spontaneous hand movement expression when the person is not aware of them. A person with AHS may reach for objects or even manipulate with precision those objects without intentionally wanting to. It was shown using functional magnetic resonance imaging that their primary motor cortex was nonetheless activated during those unconscious, unintentional, and involuntary movements (13). The contrary is also possible. For instance, simple reflexes such as the stretch reflex (also known as the Ia reflex, tendon tap reflex, and knee jerk response) are examples of involuntary, simple, stereotyped responses and movements that don't require the primary motor cortex for their expression although they can be conscious or at least consciously felt in some circumstances. That stretch reflex is elicited when a muscle and specifically its tendon is elongated suddenly. In response, the muscle from which the stimulation arises will contract ispilaterally.

When performed by a medical doctor with a small hammer tapping the quadriceps tendon or patellar tendon, its activation causes a fast contraction of the quadriceps, and hence, an extension of the leg. Given the speed of the response (e.g., 20-50 ms), it has clearly been demonstrated that the corresponding circuits, comprising only one synapse (monosynaptic), are located exclusively in the spinal cord since brain structures can't technically be involved (14). That is an example of an involuntary induced, but yet consciously felt movement. Another type of stereotyped motor behavior called the rapid eye movement (REM) may be expressed involuntary and unconsciously during sleep. Random and quick rhythmic movements of the eyes particularly during dreaming occur involuntarily (i.e., since sleeping) and thus unconsciously without a contribution of the primary motor cortex (15) although this has been recently challenged by researchers (16). Furthermore, REM can also be accompanied of violent movements of the limbs and other complex behaviors (17).

Locomotion is a highly complex stereotyped and rhythmic motor behavior that does not necessarily require cortices

Complex and very well-coordinated motor behaviors such as locomotion don't necessarily require supraspinal structures to be expressed. Convincing evidence arises from studies in decebrate or spinal cord-transected animals as well as from *in vitro* isolated spinal cord preparations. Pioneers such as Flourens (1824), Philippson (1905), and Graham Brown (1911, 1914) reported spontaneous hindlimb rhythmic stepping movements after a complete low-thoracic spinal cord transection (Tx) in cats and dogs with or without reduced afferent inputs using ether or chloroform (18-21). Grillner and Zangger (1974, 1979) have provided even more convincing evidence of a key role for spinal cord neurons in the control of locomotor rhythm and pattern generation in mammals. They showed fictive locomotor activity in hindlimb motor nerves induced by L-DOPA and nialamide i.v. in curarized Tx cats that had been completely deafferented surgically (22,23).

Several years later, selective lesions, patch-clamp, KO models, and *in vitro* isolated preparations enabled the identification of spinal locomotor neuron candidates (called locomotor CPG neurons) in the lumbosacral areas with key rhythmogenic elements in L1 and L2 (24). In humans, stimulation epidurally (ES) or intraspinally near L1-L2 segments was shown to successfully trigger stepping-like movements in patients with complete spinal cord injuries (25-28). More recently, buspirone/levodopa/carbidopa (Spinalon^{TM}) administered to completely paraplegic mice was reported to enable the expression of involuntary full weight-bearing locomotor movements on a motorized treadmill (29).

Locomotor-like activities in the muscles of patients with complete or motor-complete spinal cord injuries were also found after a single dose of Spinalon^{TM} (30). Those results provide compelling evidence that complex involuntary motor behaviors such as locomotion can, at least in some circumstances, be controlled essentially by the spinal cord. Yet, those movements can remain consciously felt by patients since vision or proprioception can provide the corresponding signals (e.g, from upper body muscles in the case of paraplegic patients).

Other highly complex stereotyped and rhythmic motor behaviors that are essentially unconscious and/or involuntary

More recently, additional complex stereotyped behaviors have also been shown to be controlled essentially by non-cortical CPG networks (24). Several CPGs have indeed been identified in brainstem and spinal cord areas. Their role in controlling the expression of complex behaviors such as deglutition, mastication, respiration, defecation, micturition, and ejaculation is increasingly being understood. For ejaculation, the pivotal role of a CPG called the spinal generator for ejaculation (SGE) essentially composed of LSt cells was found when discovering that the corresponding muscle contractions failed to be inducible in LSt cell-lesioned animals (31, 32). LSt cells were identified nearby the central canal in the lamina X and medial portion of lamina VII of L3 and L4 spinal cord segments.

The pivotal role of spinal SGE neurons in ejaculation was further supported by findings showing that microstimulation of L3-L4 segments can automatically elicit a stereotyped and well-coordinated ejaculatory motor response even in thoracic Tx animals (33). For micturition, compelling evidence of a determinant role for another spinal CPG called the sacral micturition center (SMC) was provided with experiments showing that automatic or reflex-like, well-coordinated voiding in Tx cats could be induced by intraspinal stimulation at the upper sacral level (34, 35). Specifically, using intraspinal electrodes, stimulation of the S2 segment produced bladder contractions insufficient for full voiding behavior, whereas stimulation of the S1 segment generated powerful rhythmic, well-coordinated bladder contraction and external urethral sphincter relaxation, resulting in successful bladder voiding in thoracic spinal Tx animals (36). Other CPGs involved specifically in the involuntary control of chewing, swallowing, breathing, heart rate, and defecating were identified respectively in the medulla oblongata, nucleus tractus solitaris, ventrolateral medulla, and sacral spinal cord (24).

The role of neural correlates of consciousness (NCC) in voluntary and unvoluntary movements

Although cortical structures and networks can, in some circumstances, initiate, modulate, promote, or inhibit both rhythmic stereotyped movements and volitional movements, the role of neural networks and nuclei, generally believed to underlie consciousness and awareness, remains incompletely understood. As mentioned above, although the primary motor cortex is recognized as the cornerstone of volitional movement induction, it is not necessarily activated or involved in the control of several stereotyped motor responses and behaviors. Many other areas have been postulated to play a role either direct or indirect in the expression of consciousness or consciously controlled behaviors. The premotor cortex, if stimulated electrically, has recently been shown to shut down awareness of voluntary actions (37) much like for patients with AHS (13) or anosognosia for hemiplegia (AHP).

Several other brain networks and nuclei such as the default mode network (DMN) comprising the medial prefrontal cortex, cingulate cortex, precuneus, angular gyrus, and amygdala have been associated with consciousness expression. Long-term meditation training was reported indeed to specifically stimulate NCC element such as the DMN (Rochat, 2010; Ziegler *et al.,* 2019; Polak *et al.* 2018). Interestingly, increasing evidence suggest also that regular physical activity – e.g., walking and running – can stimulate those same regions (38). Another area called the dorsal attention network or DAN (comprising the intraparietal sulcus and frontal eye fields) was recently shown to have extensive functional interactions with the DMN (39) which may suggest also a role in mindful movements.

All in all, it remains unclear the extent to which brain areas associated with conscious movement induction and consciousness/awareness expression are involved in the control of movement in everyday life. On one hand, several stereotyped behaviors (e.g, walking, chewing, defecating) are known not to absolutely require cortical activity for their control. On the other hand, several cognitive functions underlying consciousness expression such as memory, attention, focus, concentration, and executive function abilities can be improved by meditation approaches (e.g., Mindfulness Based Cognitive Therapy or MBCT and Mindfulness Based Stress Reduction or MBSR) (40-42) as well as by regular exercise (e.g., walking, running) suggesting neurofunctional links between movement and consciousness.

Concluding remarks

Obviously, further research is needed to reach consensual agreements about what conscious, unconscious and involuntary movements truly mean. NCC and corresponding patterns of global brain activity (e.g., perturbational complexity index or PCI, weighted symbolic mutual information or wSMI, integrated information or Φ, etc) have recently been proposed as meaningful assessment values of consciousness levels. Other mechanisms such as the 'holistic brain soup theory', gamma loop theory, and recurrent thalamo-cortical resonance have also been proposed to contribute to consciousness expression (11, 43-45). Yet, their role in motor control remains poorly understood.

Even if definitions are unclear and mechanisms are incompletely characterized, one thing is sure – volitional movements do not necessarily involve primary motor cortex activity whereas CPG-mediated complex motor behaviors such as locomotion can be expressed without inputs from the brain. However, since elements and mechanisms associated with the NCC can be stimulated by training (*e.g.*, meditation, physical activity (38)), it is not unreasonable to believe that we can over time voluntarily recruit them in order to bring increased awareness and consciousness to what we do either during yoga and pilates classes or in everyday duties and behaviors such as during breathing, walking, talking, eating, etc.

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