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What do *reflex* and *voluntary* mean? Modern views on an ancient debate

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Abstract Are the words *reflex* and *voluntary* useful scientific concepts, or are they prescientific terms that should be discarded? Physiologists use these words routinely in their publications, in laboratory experiments and, indeed, like most lay people, in their daily lives. The tacit assumption is that we all know, more or less, what they mean. However, the issue has a rich history of philosophical and scientific debate; and, as this article demonstrates, present-day researchers still cannot reach a consensus on the meaning of the words and on whether it is possible to draw a scientific distinction between them. The five authors present five quite different analyses. In broad terms, they split into two camps: those who equate voluntary behaviours with consciousness and suppressibility and those who view all behaviours as sensorimotor interactions, the complexity of which determines whether they are reflexive or voluntary. According to the first view, most movements of daily life are neither purely reflex nor purely voluntary. They fall into the middle ground of automatic motor programs. According to the second view, as neuroscience advances the class of reflex behaviours will grow and the class of voluntary behaviours will shrink.

Key words Reflex · Voluntary · Consciousness

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Introduction

At the 1998 Neural Control of Movement meeting in Key West, Florida, the authors presented a workshop entitled “Where there’s a will, there’s a reflex.” The workshop, organised by Jonathan Wolpaw, posed a provocative question: are the words *reflex* and *voluntary* useful scientific concepts or are they prescientific terms that should be discarded? Neuroscientists, particularly those who study motor control, use these terms freely in their scientific papers as well as in their day-to-day conversation. Every year, at least 1000 papers include *reflex* or *voluntary* in their abstracts. One might have thought that the meanings of such widely used terms are unambiguous and agreed upon by all. The workshop demonstrated that this is definitely not the case. The five authors differed markedly in their definitions, and their disagreements were echoed and extended by members of the audience in one of the liveliest debates of the meeting. This article presents the different positions of the authors, all of whom have been active in motor-control research for many years. Because the original goal of the workshop – consensus on the meanings of these terms – proved impossible, our goal in this paper is more humble and realistic. By enunciating the meanings the terms have for different researchers, we hope to identify points of commonality as well as points of disagreement and, thereby, promote better communication.

The question of what is *voluntary* and what is *reflex* has a long and fascinating history (Young 1970; Jeanne-rod 1985; Clarke and Jacyna 1987). For centuries, philosophers and scientists who expressed opinions on the issue had their books burned, were forced into exile and were even put to death (as Jon Wolpaw put it, “publish *and* perish”). Why all the fuss? Essentially two basic structures of society were directly threatened by the *free will* versus *reflex* debate: religion and the law. Stated bluntly, if all human behaviour is simply the result of chains of reflexes, as first clearly proposed by Sechenov (1863), then there is no free will, from which it is a short step to a denial of the soul and responsibility for one’s actions.

The notion of machine-like or automatic control of behaviour had its origins in treatises by Descartes (1664) and Willis (1664). Descartes proposed that sensory stimulation was transmitted to the pineal gland, which selected and opened neural tubes conveying *spiritus animus* to muscles, causing them to contract. In humans, this process was governed by the *soul*, a spiritual entity separate from and above the brain. Willis placed the connection with the soul in the corpus callosum. He proposed that the intensity of impressions arriving in the striatum, rather than the pineal gland, determined the routing of animal spirits. Willis added the notion that weak sensory impressions were reflected into movement without transmission to the corpus callosum and, therefore, without the awareness of the soul. Stronger input reached the corpus callosum and very strong input reached the cortex, the seat of memory and imagination.

A more radical step was taken by de la Mettrie (1748). He proposed an *animating principle* within the brain that mediated feelings and thoughts and coordinated the actions of a *motor principle*. There was nothing behind or above the animating principle other than the brain itself. For LaMettrie, the fact that the state of the soul depended on food showed that it was not independent of the body. LaMettrie's work was condemned to be burned and the author forced to flee into exile from the Inquisition (Jeannerod 1985). However, his ideas gradually gained support over the next two centuries, and they have been re-stated in contemporary terms many times since. But it is fair to say that dualism remains alive and well. Many, perhaps most, people believe that there is "something more to the mind" than the workings of the brain. On this view, free will and choice are assumed to underlie human actions.

The term *reflex* was first defined formally by Georgiy Procháska (1784) as a behaviour in response to an excitation, mediated by separate motor and sensory nerves. The function of reflexes was to maintain "individual conservation," later called homeostasis by Claude Bernard (1878). Many studies in the eighteenth and nineteenth centuries, notably those of Whytt (1751), Unzer (1771) and Flourens (1824) showed that the vertebrate spinal cord, after disconnection from the brain, was capable of generating automatic movements such as locomotion. In the late seventeenth century, Vieussens and Glisson had proposed that such movements were *involuntary*, though this distinction was later challenged (Jeannerod 1985). Flourens (1824) and, later, Goltz (1869) demonstrated the automaton-like nature of chronically decerebrated animals, which remained motionless unless presented with sensory stimuli. According to Brazier (1984), these experiments caused dismay because they shook the belief that the brain was the seat of the soul. This can be appreciated when one sees a re-creation of Flourens's experiments in a teaching film made by Catley et al. (1984). As a result of all these observations, voluntary movements came to be associated with spontaneous movements not requiring obvious sensory stimuli. Just where voluntary movement originated remained

problematic: Pflüger (1875), struck by the adaptive and goal-directed nature of some automatic movements of the spinal animal, claimed that the spinal cord had a psychic power and was capable of elements of perception, logic and even consciousness.

The very need for the term *voluntary* was gradually questioned. Spencer (1855) posited that reflexes were the *atoms of the psyche*, the psyche was an assemblage of reflexes and instincts were reflex assemblies consolidated by repetition and transmitted in an hereditary manner. Sechenov expanded on this theme in his famous book, *Reflexes of the Brain* (1863), proposing that all motor acts in humans as well as animals were simply chains of elemental reflexes. He argued that the appearance of spontaneity and volition was illusory and that all movements were, in principle, predicted by the history of prior events, sensory inputs and associated thoughts. The book attracted the attention of the tsarist authorities, who threatened to have it burned and its author prosecuted. Sechenov deflected his critics by protesting that free will and responsibility for one's acts were not denied by his hypothesis. Indeed, his conception of reflexes included complex responses that involved choice, as well as learned responses that his successor Pavlov would later term conditioned reflexes.

The ideas of Spencer and Sechenov were taken to their literal conclusion in the behaviourist theories of Watson and Skinner. These theories rejected all non-measurable explanations of behaviour and replaced voluntary movement with *operants*: conscious arbitrary acts which have become associated with arbitrary stimuli through learning and arbitrary reinforcement. Skinner (1985) wrote that:

cognitive scientists, claiming the support of brain science and computer simulation, have revived a traditional view that behaviour is initiated by an internal, autonomous mind. In doing so, they have misused the metaphor of storage and retrieval, given neurology a misleading assignment, ... given feelings and states of mind the status of causes of behaviour rather than the products of the causes and failed to define many key terms in dimensions acceptable to science.

Most recently, Vanderwolf (1998) wrote: "there are no clear objective criteria for assessing the existence of subjective awareness in others. This problem is particularly acute in [subjects] with impaired brain function."

Though most criticism has been levelled at the term *voluntary*, the term *reflex* has also come under fire. Goldstein (1939) pointed out the variability, state-dependence and mutability of known reflexes and concluded that none fulfilled the strict definition of an invariant response to a stimulus. This was also true of Pavlov's conditioned reflexes. The state-dependence of stimulus-response behaviours was studied by Ach (1905), who coined the term "Einstellung" (i.e. attitude, readiness to respond, set). The term *set* is now widely used to describe the task- and context-dependent modulation of simple reflexes. But mutability is not the only problem.

The term *reflex* has been used to describe not only simple stimulus-response reactions, but a variety of complex and variable motor reactions to multiple sensory inputs [e.g. Sechenov's (1863) visit to a tobacco shop, Sherrington's (1910) reflex stepping, Magnus's (1924) righting reflexes]; and, in lay terms, it includes any rapid, automatic reaction ("she reflexly caught the ball," "he had a knee-jerk reaction").

One of the most influential views on these issues is that of Hughlings Jackson (1884), who argued from his clinical observations that movements ranged in a continuum from the most automatic or evolutionarily primitive to the least automatic or most evolutionarily advanced. Primitive reflexes in humans were unmasked or released when the higher centres were damaged. The Jacksonian continuum from automatic to voluntary, with its vaguely dualist overtones (Brazier 1988), probably best encapsulates the current view of most brain scientists.

An important concept related to Spencer's atoms of the psyche, Jackson's automatic movements, and Skinner's operants emerged from studies of decerebrated and spinalized vertebrate animals in the nineteenth and early twentieth century: The brainstem and spinal cord were shown capable of generating basic rhythmical activities, such as walking, flying, swimming and breathing (Flourens 1824; Brown 1911; Grillner 1975). Brown (1911) found that, in cats, after the spinal cord had been completely isolated by transection and deafferentation, cyclical, alternating contractions could still be observed in hindlimb muscles. He, therefore, posited an *intrinsic factor* in the spinal cord that generated the rhythmical, coordinated, neural activity underlying locomotion. In 1975, Grillner coined the term "Central Pattern Generator" (CPG) for the circuitry of Brown's intrinsic factor. In invertebrates, similar considerations led to the equivalent concept of *central oscillators* (Hoyle 1975). Recent work has suggested that the strength of connections within invertebrate oscillator circuits and, therefore, the characteristics of their operation are dynamically controlled by the activity of neurones within the circuits through the action of neuromodulators (Katz et al. 1994; Le Ray and Cattaert 1997).

In 1975, Grillner wrote that "in locomotion, reflexes are prepared to operate but (are) without any effect so long as the movement proceeds according to the set central program." Taken together with Brown's finding that locomotor activity can be generated by the spinal cord isolated from both descending and sensory inputs, Grillner's statement implied that spinal CPGs may generate movements that are neither *reflex* nor *voluntary*. It also implied that the operation of CPGs was more complex and subtle than the mere playing-back of sequences of motor commands. Responses to sensory stimuli were found to depend strongly on the phase of the movement in which the stimuli were presented (Forsberg et al. 1975). A set of muscles could be activated in one phase of a movement and their antagonists in the next. The context-dependence of motor responses to sensory stimuli had, in fact, been described 70 years earlier in inver-

tebrates (van Üxkull 1904) and mammals (Sherrington 1910; Magnus 1924), but the results of Forsberg et al. (1975) still came as a surprise, because they concerned short-latency responses that might have been expected to remain constant. The complex capabilities and task-dependent response properties of subcortical (presumed unconscious) areas containing CPGs raise serious questions about categorising rhythmical movements as *voluntary* or *reflex*. As we shall see, consciousness, complexity and goal-directed choice are commonly accepted attributes of *voluntary* movements. Conversely, as Goldstein maintained, it appears that there are few if any responses to stimuli that are reproducible and invariant, which are commonly accepted attributes of *reflexes*.

The phase-dependent responses of Forsberg et al. (1975) (which, incidentally, the authors called reflexes) were elicited by stimuli applied to skin afferents which do not have monosynaptic connections with motoneurons. The phase-dependence and reversals could, therefore, be explained in terms of shifts in the balance of the many sensory, propriospinal and descending inputs that converge on interneurons in segmental reflex pathways (Lundberg 1969). Yet, even tendon jerk responses, which are largely mediated by a monosynaptic connection between spindle afferents and motoneurons, were shown over a century ago to be modulated according to the subject's motor set (Jendrassik 1885). This modulation may, of course, result from the sensitisation of muscle-spindle sensory endings by centrally generated fusimotor action (Wood et al. 1996). But even H-reflexes, the electrical counterparts of tendon jerks, which bypass the spindle endings, also turn out to be task- and context-dependent, as reported by their discoverer Hoffman in 1918. Indeed, subjects must be relaxed, perfectly still and undistracted for a series of H-reflexes to be reproducible in amplitude. H-reflexes in humans are largest in the passive, immobile subject. They become smaller during walking and smaller still during running (Garret et al. 1981; Capaday and Stein 1987). Furthermore, in the longterm, H-reflex and tendon jerk amplitudes correlate with motor training (Koceja et al. 1991) and can be changed by operant conditioning (Wolpaw et al. 1983; Segal and Wolf 1994; Wolpaw 1997). Although the purely monosynaptic mediation of tendon jerks and H-reflexes has been challenged (Burke 1983), the fact remains that these are among the simplest of all reflex responses in mammals, and yet they are far from invariant and immutable. Similar task-dependent and phase-reversal properties of short-latency reflexes have been described in invertebrates (Hoyle 1975; Bässler 1983).

Konrad Lorenz (1939), the father of neuroethology, proposed that *instinctive* sensorimotor responses of birds consisted of *fixed action patterns* (FAPs) elicited by *sign stimuli* or *releasers*. Once triggered, FAPs were performed robotically and appeared to be unmodifiable. FAPs were present in young birds born and raised in incubators, which suggested that they were genetically predetermined. Lorenz's ideas fuelled an intense, politically tinged debate on whether "nature" or "nurture" deter-

mined behaviour, a debate that continues to this day. Geneticists, for example, have refined Spencer's notion of inherited *atoms of the psyche* by suggesting that complex behaviour is made up of genetically determined components that can be revealed by genetic dissection (Tully and Quinn 1985). The notion of FAPs can actually be traced back to Descartes's analogy of the workings of clockwork automata to describe complex movements in animals. The current version of the same idea is the *motor program*, which evolved in the 1960s, along with other computer metaphors for neural function (e.g. Dewhurst 1967). Pre-programmed sequences of neural activation controlling certain innate or well-rehearsed movements were posited to be stored in the central nervous system, ready to be reproduced upon receipt of a neural trigger signal. In the sea-slug, *Tritonia*, the generation of this signal was narrowed down to *trigger group neurones* and described by the metaphor of the triggered playback of *motor tapes* (Hoyle 1975). Whether one likens the mechanisms of storage and reproduction of complex movements to clockwork automata, FAPs, motor tapes or preprogrammed subroutines, they are hard to equate either to *reflex* or *voluntary* categories.

The definitions of the "prescientific" words *reflex*, *involuntary* and *voluntary* remain in limbo not only in neurophysiology, neuroethology, psychology and philosophy, but also in the implementation of the law. Here, the matter is literally one of life and death: judgements must be made in murder cases in which the accused claim altered mind states and diminished responsibility. Perhaps the most famous recent example is the "Twinkie Defense" of a gunman who shot and killed the mayor of San Francisco and a councilman in 1978. The killer's lawyers argued that he was not at fault because he was in a zombie-like state resulting from an overdose of sweets.

In the life sciences and medicine, these words are also in constant use, whether in the laboratory, in scientific papers (for example in this journal) or in clinical practice. Given the recent progress made in the understanding of basic neurophysiological mechanisms, are we now in a better position to define these terms, or should we simply discard them? In the sections which follow, each author presents his own ideas on this question. The sections were written independently and then modified in several iterations as the evolving manuscript was circulated. The concluding section groups the separate views into two basic positions. It should be stressed that the article represents a continuing debate, with remaining differences of emphasis and opinion. We hope that the ideas presented will provoke thought and discussion in the neurophysiological community.

Volition: illusion or reality?: Arthur Prochazka

The question of the meaning of *reflex*, *involuntary* and *voluntary* is not just semantic. It goes to the very heart of our understanding of conscious behaviour. Was Sechenov right, that all actions are essentially chains of reflex-

es and that volition is an illusion? When humans claim they can choose to act or not, is this choice not a choice at all, but simply a consequence of the individual's neural wiring and all prior inputs and outputs? I will argue that the terms *reflex* and *voluntary*, whose current lay meanings are essentially the same as they were in ancient Rome, will continue to be used extensively in the vernacular as well as in science because they fulfil a need to differentiate between behaviour which appears to be "chosen" from that which appears to be automatic and hard to suppress. "Appears to be" is key, allowing us to sidestep the free-will debate. Given that many neurophysiologists, including all of the authors of this paper, have used *reflex* and/or *voluntary* in the past and will probably continue to do so in the future, it is useful to collate all the meanings of the terms as they are currently used by movement-control researchers. For practical purposes, I will adopt the view that "we must believe in free will, we have no choice", even if this is only the illusory free will of Sechenov. I will also touch on some interesting parallels in the terminology of modern control theory.

Linguistic definitions

The Oxford elementary latin dictionary says that the Roman poet Ovid used *reflex* in the sense of "turn back, bring back." Virgil wrote "*animum reflexi*": brought my thoughts back (to her). Substitute "feed" for "bring" and we have the neologism "feedback", which replaces *reflex* in control systems theory. As we saw in the Introduction, when applied to animal movement, *reflex* is not only used in relation to responses of a simple feedback loop. It is also used in relation to complex responses to sensory input, such as those in locomotion, for example. The word *voluntary* also derives from the Latin *volo*: to will, wish, want, desire, intend. This word is more difficult to pin down than *reflex*, as John Rothwell shows very clearly in his section below. And if *voluntary* is hard to pin down, then it follows that *involuntary* must be too.

At the Neural Control of Movement workshop, I presented the main attributes of each of the above terms that I had come across in the literature. The idea was that, if we could all agree on the most important attributes and their relative weights, this would allow any particular behaviour to be assigned a numerical score based on the relative truth of each attribute and the resulting sum of weights. However, the notion of deriving a precise numerical score from a set of imprecise, qualitative judgements did not appeal to my colleagues then or since ("a classic example of bad pseudo-science" was one comment). Yet one thing did emerge from the exercise: particular examples of movements that most people would not hesitate to classify as pure reflexes, for example the eye blink response or the tendon jerk elicited in a resting subject, always scored *some* marks in the voluntary category, the reason being that these responses could be controlled or modified to some extent and they could be

consciously perceived. *Suppressible* versus *irrepressible* and *conscious* versus *unconscious* were identified as key attributes of voluntary behaviours. By the same token, behaviours that are thought of as purely voluntary, such as self-paced hand movements, are often performed automatically (a reflex attribute) and unconsciously. These, therefore, scored some points in the *reflex* category. The other attributes of *voluntary* versus *reflexive* behaviour were *self-generated* versus *stimulus-bound*, *unpredictable* versus *predictable*, *complex* versus *simple* and *learnt* versus *innate*.

If language were logical, *involuntary* would have exactly the opposite meaning and attributes to *voluntary*. However, historically, *involuntary* has been used to describe sequences of goal-directed movement often arising spontaneously, for example in decerebrate animals or in dyskinetic humans (see Rothwell's section). In fact, the term *involuntary* has been used variously to describe spontaneous or evoked, simple or complex, predictable or unpredictable and learnt or innate movements. These attributes, therefore, include *reflex* and *voluntary* categories as well as the ground between. Psychologists have long spoken of a transition from *cognitive* through *associative* to *autonomous* phases of motor learning (Schmidt 1988). Alternatively, one could think of this transition as being from *voluntary* through *involuntary* to *reflexive*. It is interesting to note that concert musicians try to limit their conscious involvement during the performance of well-rehearsed pieces, because too much attention "gets in the way." In other words, they strive to take the *voluntary* out of their performance. Schmidt's analysis of how movements become automatic invokes both *pre-programming* and *specialised processing* (fixed action patterns, subroutines). In his section below, John Rothwell stresses the automaticity of most movements of daily life. The *involuntary* category, because it highlights automaticity, but not necessarily stimulus-bound predictability, seems more appropriate than the *reflex* category to describe many such movements. Libet et al. (1983) reported that, even in the most voluntary act one can think of: a spontaneous, free, isolated movement of the human hand, subjects only became consciously aware of the onset of the subjective feeling of "wanting" or "intending" to act about 200 ms *after* the first detectable changes in cerebral activity. However, Dennett (1998) has made the interesting point that consciousness itself is not instantaneous, but rather develops over time. The conscious appreciation of the onset of neural generation of a movement may evolve along with the movement, and it may, therefore, be wrong to expect a precise moment when we become conscious of a movement.

If we accept that the neural onset of voluntary movements precedes full-fledged conscious appreciation, then we must either conclude that *all* movements have an involuntary origin, or that the attribute of *suppression* is more discriminative than the attribute of *consciousness*. When John Rothwell says below that the essential part of the definition of *voluntary* is "whether or not we can take control of a movement," the word *we* presumably

refers to the conscious brain mechanisms that can choose to suppress (or not suppress) a movement in advance. Yet a problem remains. If one thinks back over the last few seconds, one can usually identify one or two "absent-minded" movements one just made. These movements could in principle have been suppressed, but often we cannot be sure. Were they *voluntary*, *involuntary* or *reflexive*?

Control-systems analogies

Brains are control systems par excellence, so it is worth considering the structure of *artificial* control systems in relation to the question of motor behaviour. As mentioned earlier, the closest control-theory equivalent to the word *reflex* is *feedback*. The compensation for a disturbance in a simple control loop is equivalent to a simple reflex response. Yet engineers do not think of such corrections as atoms, elements, or primitives of a feedback-system's behaviour. Rather, they view such a system as continuously and smoothly minimising differences (errors) between desired and actual values of controlled variables, whether the errors result from external perturbations, inadequacies of actuators or varying properties of loads. Physiologists, usually constrained to probing the nervous system from the outside, have traditionally applied discrete perturbations and measured responses to them. Some responses were quite complex, and so it was a logical step for Herbert Spencer (1855) and Sechenov (1863) to propose that all complex behaviours are simply assemblies or chains of reflexes, the completion of one triggering the onset of the next. But from a control systems point of view, this is an awkward way of looking at the continuous operation of a system with interdependent feedback loops and control rules (this point is made in a different way by François Clarac, below).

The word *voluntary* is not used in automatic control systems, but some close cousins are: *desired input*, *command* and *set point*. In robotics, complex movements are often controlled by a computer, which breaks tasks down into portions or subroutines called from a main executive program. Subroutines are triggered by the achievement of goals detected by sensors. They could be equated to FAPs or preprogrammed sequences of movement. In a remarkable recent study, Plum et al. (1998) used electroencephalography, magnetoencephalography and positron-emission tomography in chronically unconscious persons to reveal small regions they termed *brain modules*, whose activity was associated with isolated verbal utterances or "coordinated, non-purposeful, non-dystonic" limb movements (i.e. motor subroutines).

Subroutines may operate indirectly by adjusting the gains of automatic feedback loops according to predetermined *gain schedules*. A biological analogy is the phase-dependent modulation of sensory-evoked responses in the locomotor step cycle. In adaptive control systems, gain parameters are adjusted to maximise some performance criterion (cf. adaptation of reflexes to repeated

stimuli). In predictive control systems, gains are adjusted in advance of expected events [cf. *behavioural set*, in which an animal anticipates responding to sensory stimuli: Prochazka (1989)]. In multivariate systems such as production-line controllers, the executive program and subroutines may make IF-THEN choices based on input from numerous sensors. This is analogous to the IF-THEN logic that appears to underlie locomotor control in different species (Prochazka 1996). Along the same lines, Bässler (1983) has proposed the metaphor of a “parliament” of sensory processors that “vote” for different responses, the result being decided by a weighted sum. This is essentially how neural net or fuzzy logic controllers operate.

Consider the behaviour of complex software. We have all been irritated by a program “doing its own thing.” The complexity of the process has made the computer’s behaviour appear intentional, not to say malevolent. If today’s software is complex enough to give passable illusions of volition, then for the vastly more complex human brain, the illusion is to all intents and purposes complete, i.e. the illusion is the reality. If we accept this, then words like *voluntary*, *attention* and *consciousness* can in principle be defined scientifically.

We saw above that predictability and automaticity were key attributes of reflexes. Yet Goldstein (1939) and many others since have pointed out that responses described as reflexes are often mutable and dependent on overall state and context. This seemed to invalidate the idea that neural behaviour could be dissected into simple, well-defined operations (see also the sections by Clarac, Loeb and Wolpaw). However, a present-day engineer analysing the responses of a multiple-input multiple-output (MIMO) control system is not surprised when the system’s responses vary according to state. This is the expected consequence of processing multi-sensory input according to context-dependent rules (IF-THIS-AND-THIS-THEN-THAT). Thus, unpredictability and state-dependent complexity do not of themselves preclude a deterministic, feedback control structure. Neural-net controllers learn complex behaviour by forming internal connections that, in their detail, can become extremely difficult to disentangle. The operation of these machines is best approached by considering their learning algorithms and the input-output rules that emerge rather than the operation of elemental components and connections. By analogy, as mechanistic descriptions of brain behaviour advance, the terminology should become less polarised: The words *reflex* and *voluntary* will presumably give way to the language of conditional logic and complex systems (however, see Wolpaw’s alternative conclusion).

Origin of neural commands

From the above, reflexes are understood to be stimulus-bound, while voluntary movements are self-generated. It is, therefore, of interest to examine the sites in the CNS

that commonly give rise to the commands to activate muscles and to ask which, if any, of them do so spontaneously:

1. Posture and locomotion. In chronic decerebrate and spinal animals, although locomotion, postural adjustments to perturbations and responses to irritants can be controlled by spinal and brainstem mechanisms, such movements rarely arise spontaneously, as is starkly clear, for example, in the video film of Catley et al. (1984). The spinal cord and brainstem thus tend to operate as trigger- or stimulus-bound mechanisms with adaptable sets of control rules that vary in complexity, but which, in essence, are machine-like, i.e. they occupy the *involuntary* middle ground of the Jacksonian continuum.
2. Homeostatic drives. Deviations from set points of internal variables, e.g. hypercapnea, hypoglycemia and electrolyte imbalance, provide powerful and eventually irresistible drives for motor behaviour; such as breathing, eating, drinking and locomotion. Such deviations are sensed in the hypothalamus and other midbrain or brainstem areas, that in turn project to parts of the CNS more directly connected to motor circuitry. The movements that result often have identifiable stimulus-bound origins, but, although they are usually performed automatically, they can be consciously perceived and suppressed, at least up to a point. This combination of attributes also best fits the *involuntary* category.
3. Active touch. Exploratory movements form a major part of many animals’ daily activities. It is often difficult to identify specific stimuli that elicit these movements, and, in general, the brain areas that first become active are hard to pinpoint except in restricted and artificial tasks starting from rest (e.g. Deecke et al. 1969; Kristeva and Kornhuber 1980; Libet et al. 1983; Plum et al. 1998). As mentioned in the summary, Jeannerod (1985) suggested that complex nervous systems need a constant flow of information in order to organise themselves to act. On this view, voluntary movement is a process of self-generated *active touch*. To borrow from Pinker (1997), humans are inform-avores, actively eliciting and analysing sensory experience. Yet, we must remember Sechenov’s (1863) argument that no movements arise *de novo*. Ultimately, the most *voluntary* of movements can also be viewed as reflexive because they must derive from the individual’s environment, prior history and neural wiring.
4. Attention, consciousness. If conscious awareness is an important attribute of voluntary movement, attentional mechanisms must be too. Crick (1984, 1995) has suggested the notion of a *spotlight of attention* directed around the brain to illuminate particular sensory or cognitive processes. This interesting metaphor for our restricted ability to “foveate” or pay attention to only one or two things at a time presupposes a control centre that has been variously placed in the thalamus, basal ganglia and anterior cingulate gyrus. The

control centre supposedly directs or orients the spotlight's beam and attends to the illuminated area (Posner and Dehaene 1994). Baars (1998) defined attention as the process of *selection* of the spotlight's target and consciousness as the ability to *report on* the target. People with alien hand or Tourette's syndrome (discussed by Rothwell below) can certainly report on their involuntary movements, so on Baar's definition, if conscious appreciation of movement is a necessary attribute of volition, it is clearly not sufficient. The alien hand syndrome also happens to be a crucial part of Crick's (1995) argument that free will is located in the anterior cingulate gyrus. This was based in part on a patient with a lesion in the right anterior cingulate who also had a lesion in the corpus callosum, which disconnected the hemispheres. He could only stop his left-hand grasping by shouting "let go." John Rothwell describes similar patients in his section below. Notice that Crick's interpretation of volition here is a conscious, verbalised output by the left hemisphere that "takes control" of an automatic response of the right hemisphere (see Rothwell below) and modifies the response *during its execution* (see Loeb below). On this view, the necessary and sufficient attributes of volition are suppressibility and conscious attention (as defined by Baar). But even this does not really suffice. Consider a subject making a self-paced arm movement. The subject claims to be conscious of the movement and can suppress it. But is this really true of every aspect of the movement? Arm movements are preceded and accompanied by phasic postural activity of muscles in the back (Zedka and Prochazka 1997; Zedka et al. 1999). Unless they are prompted, subjects are unaware of this activity and are unable to suppress it without also suppressing the arm movement. If an obligatory part of a motor act is neither chosen nor perceived, it is hard to maintain that the act as a whole is completely *voluntary*.

Sensory modulation as a manifestation of shifts from reflex to voluntary

Strangely enough, the ability to detect and rank cutaneous and proprioceptive inputs is reduced during repetitive arm movements, just when one might imagine they would be most required (Collins et al. 1998; Wise et al. 1998). Similarly, static fusimotor drive seems to *reduce* the responsiveness of muscle spindles during routine locomotion. On the other hand, fusimotor drive is *increased* in novel or difficult motor tasks (Prochazka 1996). Perhaps the proprioceptive system is providing us with a glimpse of internal shifts of conscious attention in the brain as movements shift back and forth along the *reflex-voluntary* continuum.

Conclusion

Some physiologists would say that there is really no problem in any of this: stimulus/response actions that subjects carry out according to instruction are *voluntary* and responses that the subjects cannot modify according to instruction are *reflexes*. If asked, subjects would presumably report that they consciously controlled the *voluntary* behaviours, but not the *reflex* ones. But even the most "voluntary" of such tasks, reaching out and grasping an object, may start unconsciously (Libet et al. 1983), be preceded by unconscious postural adjustments and involve crucial size judgements of which the subject is not only unaware, but even perceives and reports incorrectly (Jeannerod et al. 1995; Haffenden and Goodale 1998). Most movements we make in our daily lives are performed with little or no conscious attention, and in many cases it is difficult to know after the fact which of them we could or could not have suppressed. On the definitions above, this means that most movements are *involuntary* (or, as Loeb would have it, *pre-programmed*). It follows that there are few, if any, purely voluntary (suppressible and conscious) or purely reflexive (stimulus-bound and irrepensible) movements.

To get back to the provocative question posed at the beginning of this article, my basic position is that *most* scientific words have prescientific origins. The words *reflex*, *involuntary* and *voluntary* are no exception. One could insist that, along with terms like consciousness and free will, they are scientifically undefinable and, therefore, useless. Yet, it is obvious that they will continue to be used by scientists as well as lay people for a long time to come. And, in my opinion, they will continue to provide useful scientific insights. One of these is that our difficulty in classifying motor acts as voluntary or involuntary is the inevitable consequence of the overlap in the attributes that describe them as well as the brain mechanisms that control them.

The concept of reflex and automatic control of movements: Francois Clarac

In general, it is considered that lower vertebrates and invertebrates perform *automatic* and not *voluntary* movement; the latter being equated with "spontaneous activity," a very vague term. At first sight, the term *reflex* seems to be appropriate and able to explain most of the reactions of animals. However, in this section, I will try to demonstrate that it is, in fact, a very confusing and inadequate descriptor in most cases and should be replaced by the more general term *sensorimotor interactions*.

The term *reflex* had been used in the general sense of an input-output "reflexion" in several countries for two centuries before the development of neurophysiology as we now know it (Fearing 1970). It was applied rather loosely to a whole variety of motor behaviours. Sherrington (1906) took a more precise, physiological approach in his studies on reduced preparations, defining a

reflex mechanism as the simplest element of the nervous system able to produce unitary, elementary reactions. To qualify as reflexes, responses had to be perfectly reproducible, graded with respect to stimulus intensity and they had to occur at a specific time after the stimulus. However, these conditions are hard to meet given the complexity of sensorimotor integration in most motor acts. In the sensory context, the term is used variously in relation to feedback, afferents, servo-mechanisms and sensorimotor transformations. In the motor context, some complex activities are termed reflexes and others, originally named reflexes, are now termed motor reactions, synergies or strategies. One classical example of confusion is the persistent habit of speaking of a locomotor *behaviour* separately from a scratching *reflex*, even though the underlying mechanisms are more or less the same.

As we have seen, reflex responses were originally characterised by their automaticity and repeatability. As time went by, the list of responses classed as reflexes became more and more extensive. However, neurophysiological explanations remained primitive. The CNS was essentially a “black box,” in which it was assumed that the circuitry of reflex responses was contained. The idea gradually developed that the CNS operated as an ensemble of interconnected and adapted reflex modules (Sechenov 1863). In the spinal cord, the reflexive nature of muscle responses to stretch received strong support and acceptance with Lloyd’s (1943) demonstration of the monosynaptic reflex arc involving two sets of neurones: muscle-spindle afferents and motoneurons.

In contrast to the emphasis on the sensory control of motor acts, the concept arose of an *intrinsic factor* (Brown 1911) or CPG (Grillner 1975), consisting of neural circuitry within the CNS that is able to shape and pattern motor activity without descending or sensory input (Wilson 1961; Delcomyn 1980; Getting 1983, 1989; Barnes and Gladden 1985; Selverston 1985; Rossignol et al. 1988). More recent studies have shown that four building blocks are likely involved in the structure and function of pattern generating networks: intrinsic neuronal membrane properties, properties of synapses, neuronal connectivity and neuromodulators (Harris-Warrick et al. 1992; Calabrese 1998).

Recent experiments on both invertebrates and lower vertebrates have expanded our knowledge of reflex control. In particular, neuronal connectivity has been elucidated in great detail with intracellular recordings. In arthropods, the equivalent of the mammalian monosynaptic stretch reflex, the *resistance reflex*, has been studied in detail (Burrows 1975; El Manira et al. 1991). It was shown that resistance reflexes varied not only in intensity, but also in sign, according to state or motor task. Burrows (1992), studying the locust femoro-tibial joint, found that the circuit underlying the resistance reflex is composed of a mechanoreceptor, the femur-tibia chordotonal organ, two types of interneurone (a sensory spiking interneurone and a premotor non-spiking interneurone) and the motoneurone. In the stick insect, Bässler (1983)

and Büschges et al. (1994) also found that the sign of the reflex depended on the state of the preparation. If the animal was inactive, the reflex corresponded to negative feedback. If the animal was active, the reflex switched to positive feedback, assisting rather than resisting movement (see also Prochazka et al. 1997). Assuming that the same interneurons were involved in the two conditions, the modification might have been due to a change in the weighting of parallel excitatory and inhibitory synaptic inputs from the sense organ; in other words, the eleven non-spiking interneurons were playing a completely different role in the two situations.

In the crayfish thoracic *in vitro* preparation, the chordotonal basal coxal organ (CBCO) reflex acting on the depressor muscle also has two modes of behaviour. At rest, the released sensory fibres act monosynaptically on the depressor motoneurons, inducing a resistance reflex (negative feedback). When the preparation becomes rhythmic, as in locomotion (induced, for example, by adding a muscarinic solution to the bath), the CBCO reflex becomes an assistance reflex [positive feedback: Clarac and Cattaert (1996)]. We suggested that this is due to two phenomena: (1) signals transmitted by the sensory afferents are centrally filtered by presynaptic mechanisms that block the resistance reflex, and (2) the connectivity of some interneurons changes, inducing the assistance reflex (Le Ray and Cattaert 1997). In the stick insect, the first mechanism enhances the role of parallel antagonistic pathways, while the second causes a switch between monosynaptic and polysynaptic circuits. The essential point is that, in both cases, the response evoked by the same sensory message is completely changed by a central program.

Except for a few movements that can be performed completely open loop, the great majority of movements derive from the activity of central structures, which are continuously fed input from sensory afferents (Bush and Clarac 1985; Prochazka 1989; Pearson 1993). This means that the notion of an ensemble of afferents interacting with the motor command is difficult to reduce to a succession of reflex pathways. Afferents act continuously at each level of the hierarchical system, i.e. in each pathway of the command. In a given behaviour, like locomotion, afferents have been shown to have the following involvements:

1. Triggering: e.g. in insect flight, the simultaneous stimulation of the setae of the head and the suppression of the local tarsus contact occurring during a jump is enough to induce flight.
2. Controlling cyclical movements: the two main phases of locomotion are continuously controlled by different types of afferent. Sensory afferents closely linked to the central network can affect its operation, as in the case of spinal-cord intramedullary stretch receptors of the lamprey, which stabilise rhythm generation during swimming (Grillner et al. 1995). In the *Xenopus* embryo, an external stimulus can entrain the swimming rhythm via specific spinal sensory inter-

neurons that control sensory transmission in a phase-dependent manner (Arshavsky et al. 1993).

3. Controlling the cessation of movement: afferents contribute to the return to a resting posture.

In summary, afferents reinforce the ongoing motor program (Pearson and Ramirez 1997) and are of great importance for switching from one phase to another, e.g. from swing to stance and vice versa (Bässler 1983; Clarac 1991).

It is clear from the above that the term *reflex* in fact covers a wide range of sensorimotor interactions, and its meaning has changed as motor-control theories have evolved (Stein et al. 1997). If we wish to be strictly accurate, the term *reflex* should be restricted to two situations:

1. In normal behaviour, reflexes are simple, fast reactions to the environment. The term should be confined to the simplest input-output reactions mediated by monosynaptic (or oligosynaptic) pathways at the lowest level: i.e. at the motoneuronal level. Reflexes should be viewed as elements of feedback control, which each species possesses to react automatically to the environment. The use of the term *reflex* in the phrase “monosynaptic stretch reflex” is appropriate, whereas, when we consider polysynaptic responses such as assistance “reflexes,” the term *reflex* is inappropriate because of the complexity of the neural network involved.
2. The experimenter can induce a reflex artificially. In a given preparation, he/she ideally stimulates just one modality of receptor, the subject being at rest. This situation occurs rarely, if ever, in tasks of daily life. However, clinicians deliberately evoke such a response to test a patient’s neurological condition. In other words, the term reflex is useful when it is considered as a tool for testing the CNS. Reflexes then reduce to informative tests of CNS state. A reflex might be seen as a physiological “scalpel”, permitting entrance into simple workings of the CNS, while not being a distinct and separable element when normal movements are considered. Thus, although the understanding of motor behaviour has benefited from reflex experiments, the normal functioning of the CNS, in which many afferent messages are integrated, should never be viewed as reflexive behaviour, even in the case of the “automatic” movements of invertebrates and lower vertebrates.

Dealing with reflexes that are learned or consciously adapted: Gerald E. Loeb

Psychologists and philosophers are generally content merely to name things and study the relationships between the named constructs. Physiologists generally give names when they think, believe or at least hope that those names have a one-to-one relationship with an underlying physical structure or at least mechanistic rela-

tionships. Reflexes were originally identified on the basis of motor outputs that were produced by isolated spinal cords; voluntary behaviours required brains, particularly the cerebral bits associated with consciousness (whatever that now means). Sherrington’s interest in the reflex as the “unit” circuit from which more complex behaviours could be composed is a strong example of this mechanistic orientation. Clarac would preserve the experimentalists’ association of reflex with an oligosynaptic circuit, but abandon its use in the decomposition of voluntary behaviour. Much recent work, including that summarised at the Neural Control of Movement workshop, questions the automaticity even of those oligosynaptic circuits while pointing out the potential for automaticity in voluntary behaviours. The question posed to the workshop was whether that leaves any room for the words themselves.

The mechanistic relationship that I have been studying involves the limits of reflex plasticity. Over the past few decades, we have learned to accept the notion that even *involuntary*, *unconditioned* and *segmental* reflexes have their gains altered as part of conscious behaviour (as pointed out as early as 1939 by Goldstein). Prochazka traces the roots of *behavioural set* and its sister concept of *gain scheduling* in control engineering. Not only do these gains have more than one value, but the values themselves are subject to plasticity, such as that associated with recovery from injury (Whelan and Pearson 1997). More importantly, Chen and Wolpaw (1996) have shown that the nature of these alterations can themselves be learned and unlearned, albeit with a lot of feedback and practice. Even that might be seen as an embellishment of reflexes that still exist in a given species as default circuits that are genetically specified in some primordial sense. Against that explanation is the extreme variability of certain well-developed reflex patterns that seem to arise spontaneously in different individuals with no identifiable features in their physiognomy or behavioural training. The short-latency cutaneous reflexes produced in some muscles of the cat hindlimb during locomotion are particularly pleiomorphic (Loeb 1993).

To explore the nature and source of this reflex variability, I have tried to dissociate the locomotor activity of the muscles from their reflex contributions by using the technique of tendon-transfers to change the mechanical actions of certain ankle muscles during early development of locomotion. The results are consistent with prior evidence that the locomotor pattern generator is fairly robust in the face of such musculoskeletal modifications (Sperry 1945; Forssberg and Svartengren 1983), but I observed rather dramatic asymmetries in the cutaneous reflexes of the two limbs, more or less in proportion to the persistence of the surgical modifications (Loeb 1998). This suggests to me that at least some quite low-level “reflexes” are essentially “learned” behaviours of the spinal cord. Perhaps they could be subsumed into the notion of *conditioned reflexes*, but the absence of a clear association between the observed reflexes and an invariant *unconditioned reflex* would seem to stretch the

Pavlovian roots of that word beyond the acceptable. Furthermore, at least some of the limb reflexes that can be created in conventional *conditioned-reflex* paradigms appear to depend on the cerebellum rather than the neocortex (Kolb et al. 1997), which is not the organ favoured by most of those searching for the seat of consciousness or voluntary behaviour.

At least some of the semantic difficulty with the terms *reflex* and *voluntary* may be self-inflicted from two gratuitous dichotomies. First, the panellists at the workshop were asked to decide whether these terms were “useful” or “prescientific”, as if these choices were mutually exclusive. As Prochazka suggests, even those who find them to be prescientific will continue to use the terms as convenient shorthand jargon, which makes them at least useful. Further, all the things society would really like us scientists to explain have been around long enough that the words for them are necessarily prescientific. Second, the title implied that all behaviour must be either *reflexive* or *voluntary*. Again, Prochazka identified a middle ground which he called *involuntary* (which has the decided disadvantage of creating two contentious boundaries where only one existed before).

I would like to try to improve the working definition of *reflex* by redefining the middle ground as *preprogrammed* rather than *involuntary* and by emphasising timing, which is often critical for experimental definitions of reflexes. For me, a reflex is a triggered response to a stimulus that cannot be modified voluntarily *during its execution*. This is different from Rothwell’s phrase “influence the task at hand”, which leaves open the question of conscious gating of reflexes before they occur. In order to agree with current usage, the concept of *reflex* must include all manner of consciously determined or unconsciously learned changes in the reflex that is actually elicited. It should, however, exclude behaviours that are often largely automatic, but *could* be modified during their execution, such as walking. Those behaviours (which include most of those cited by Rothwell) would go into the middle *preprogrammed* category, which recognises that they can proceed without conscious intervention, but that they unfold slowly enough to permit them to be aborted or modified “on-line” should circumstances warrant. I would then reserve *voluntary* behaviour for those activities that proceed only under conscious control. This would include the initiation, but not the maintenance of many preprogrammed behaviours. Note that these terms are hierarchical in that preprogrammed behaviours will often be built upon reflexive behaviours (à la Sherrington) and voluntary behaviours will often be built upon both, but a lower-level behaviour cannot contain a higher one. It also relates to the concept of voluntary reaction time, which essentially limits the duration of an activity that can be considered to be reflexive under this definition.

As for the more philosophical arguments regarding free will, those of us unwilling to embrace mind-body dualism must accept the pragmatist’s compromise. Consider a physical analogy. We have no difficulty using the

classical gas laws to understand the emergent behaviour of a cylinder full of gas molecules, even when we know that this is simply a probabilistic approximation of the deterministic interactions among individual particles. At an even deeper level, we learn that these particle interactions are themselves not fully deterministic because they are only a probabilistic approximation of their underlying quantum mechanics. The designer of steam engines is happy to rely on the general utility of the gas-law approximation, and the designer of laws in jurisprudence is happy to rely on the general utility of the free will approximation. Neurophysiologists will describe the activities of neurones that underlie the behaviours that we attribute to free will, but this will not put psychologists, philosophers or lawyers out of business. At the limit, the underlying noise and uncertainty of quantum mechanics will save even the most ardent reductionists from Maxwell’s demon, Schroedinger’s cat and (let us hope) the Twinkie Defense.

What, if anything, is voluntary?: John Rothwell

The term *voluntary* is as hard to define as *reflex*. Most physiologists seem to steer clear of a direct definition, perhaps because of an ingrained fear of being drawn into philosophy. In many cases, the definition of *voluntary* defaults to what remains after *reflexes* have been defined. The problem seems to be that accepting the notion of *voluntary* is perilously close to admitting the concept of free will, and, as both Prochazka and Loeb point out, these are deep waters indeed. If free will is intangible, it is therefore unmeasurable and beyond the scope of scientific investigation.

I will propose that we step back from philosophy and use the term *voluntary* in its vernacular sense. In fact I argue that this “prescientific” sense is probably a much better and workable definition of *voluntary* than our efforts at a scientific definition. Let me begin by looking at possible physiological definitions of *voluntary*. To many of us (see Prochazka’s definitions above), it means a movement that is goal directed and under complete conscious control. It is a movement that is initiated by internal effort, and, if it is affected by sensory input, it is only because this input has first been consciously evaluated and a wilful decision taken about how to continue the task. The problem with this definition is that very few, if any, of our movements are produced in this way. I would argue that complete conscious control of any movement from its initiation to completion is so rare as to be a negligible part of normal motor control. More often than not, we simply decide when to start a movement and make a decision later about its success. Running the task is automatic.

For example, at the behavioural level, how often do we get in the car and decide to drive home from work and then be so engrossed in solving a problem at work that we cannot recall the route we took back home? This may be a complex example, but it is reflected at a simpler level by some clever physiological experiments of

McCloskey and colleagues (Taylor and McCloskey 1990, 1996). They used the phenomenon of backward masking to show that subjects could react to stimuli that were not consciously perceived, even when this involved choosing a course of action dependent on the type of the (non-perceived) stimulus. The only precondition was that subjects had to be trained to know what to do if they consciously perceived the same stimuli. In other words, they had to prime their motor system voluntarily, and, once this was done, the program could be selected and run automatically. In a recent example, Valls-Solé et al. (1999) provided evidence that, under certain circumstances, brainstem mechanisms could release voluntarily prepared responses without involvement of the cerebral cortex. Again, the implication was that, once the motor system was set up to go, then movements could be run automatically and without voluntary intervention. Perhaps the only time that we are in moment-to-moment control of our own movements is in the initial stages of learning a completely new task.

The idea that we are voluntarily in control of a movement because we have made the initial decision about what to do is satisfying, but is it always the complete truth? To phrase it in a different way, in order to exclude the introspective element from the question, can we say that, if a movement appears to an external observer to be made towards some predefined goal, is this cast-iron evidence of voluntary control? In my opinion, the answer is not clear. How many times during writing this piece have I scratched my nose, shifted my seat, or even got up to make coffee without any conscious effort of will. Indeed, in many cases, I will only have noticed that I made any of these movements after they have occurred.

We do not need to rely on introspective effort to prove this point, neurology can provide very useful examples. Alien limb syndrome is a rare condition that sometimes occurs after a stroke to the frontal areas of cortex (Doody and Jankovic 1992). Patients complain that they have no voluntary control of the contralateral arm (or leg). It may reach out to grasp objects near to the patient without warning and act as if controlled by some external agent. Patients often resort to sitting on the hand to stop the arm from moving. The mechanism is not clear, but may involve release of activity in some visuomotor reaching circuitry. However, it does illustrate just how complex totally involuntary movements can be. It is important to note that patients are consciously aware that their arm is moving: this is why the movements irritate them so much. Although they are aware of the inputs produced by the arm, they are not in control of the outputs that are telling the arm to move. My argument is that many of our daily movements are made quite automatically. They may be goal directed *and* they may start without our conscious intervention, yet, despite this, the man in the street would think us crazy if we tried to insist that, for 99% of his waking life, he had no voluntary control over his own body.

The definition of a voluntary movement as a voluntarily initiated and controlled motor act is so limited as

to be useless. We need a better definition of *voluntary* that corresponds to our own perception that we are in control of our own bodies. For this, I go back to the “prescientific” usage. I propose that an essential part of the vernacular definition of voluntary is whether or not we can take control of a movement. The importance of being able to suppress unwanted movements is well illustrated by patients with Gilles de la Tourette’s syndrome. These patients have involuntary tics that can range from myoclonic jerks of a limb to explosive vocal outbursts. A crucial, and diagnostic, feature of these tics is that they can be suppressed by voluntary effort of will for short periods of time (Jankovic 1997). However, after a while, the urge to move becomes uncontrollable, and a period of voluntary suppression is usually followed by a florid display of ticcing.

The point is that our concept of *voluntary* involves active suppression as well as initiation and control of movement. In fact, I think that our intuitive idea of what constitutes a voluntary movement depends entirely on whether we think we can influence the task in hand. It does not matter whether an ongoing movement is being performed consciously or is directed towards some external goal. If we can interrupt it, we can say we are in voluntary control. Defining *voluntary* like this puts it outside the conventional scheme that grades movements from reflex to automatic to voluntary. All movements become automatic or reflex. *Voluntary* is simply a measure of how well we can influence them.

The layman’s definition of voluntary works well up to this point. However, I have to admit that it begins to fail if we probe a little deeper. Is it possible to know whether a movement was voluntary or not just by observing it from outside, or do we always have to rely on the report of the individual who was moving? If the latter, then how do we verify that this is true? Can we measure some sign of volitional involvement, perhaps in the pattern of brain activity? All this brings us even closer to free will and is perhaps an excellent place to take an intellectual pause.

Old words in a new science: Jonathan R. Wolpaw

As Prochazka observes in his section, the terms *reflex* and *voluntary* have been around for a long time and will doubtless continue to be used in everyday life and in the law to distinguish between behaviour that appears to be chosen and behaviour that appears to be inevitable. However, this fact does not guarantee these terms a useful role in contemporary neuroscience. Many other old terms that are still used in other contexts have disappeared from science. People still refer to sunrise and sunset, but the idea that the sun moves around a fixed earth disappeared from astronomy in the fifteenth century. *Impetus* remains a useful term, but not in physics, where it was long ago displaced (as it were) by *inertia*. People still learn things “by heart,” though we no longer agree with Aristotle that the heart is the organ of memo-

ry. *Sanguine, phlegmatic, choleric* and *melancholic* are handy adjectives for describing people and their personalities, but they no longer represent the theoretical foundations of clinical medicine as they did in the Galenic physiology that dominated medical science until the Renaissance. Other terms have survived in science, but with new meanings. *Earth, air, fire* and *water* are still scientifically useful terms, but they are no longer the four elements out of which all matter is formed.

Neuroscience is blessed, or cursed, with numerous ancient terms that will continue to survive outside science whatever their fate within science. Many came originally from introspection, from each person's perception of events inside him or herself and from the inferences this prompted about events in others. Introspection led to the postulation of an entity called the mind, or the soul, that had functions, or faculties. The list of these faculties differed from one description to another, but always included in some form consciousness and volition. From these concepts came the original meanings of reflex behaviour and voluntary behaviour. Voluntary behaviour was a product of the mind, or soul, and was preceded by and accompanied by consciousness. Reflex behaviour was neither. Until the early nineteenth century, scientists were comfortable with this analysis based on introspection and believed that the production of voluntary behaviour and the production of reflex behaviour were two completely separate brain functions. In his famous treatise of 1784, Georgiy Procháska defines these two different functions of the nervous system. He explains that the nervous system is first "the seat of the rational soul, and the link by which it is united to the body," it is "the instrument by which the soul ... produces its own actions [i.e. voluntary behaviours]." Second, according to Procháska, the brain also possesses "the singular faculty of exciting in the human body various movements without the consciousness or assistance of the soul [i.e. reflex behaviours]."

Contemporary neuroscientists seldom mention the soul in their analyses of brain function, but as the presentations in this article indicate, the dichotomy summarised and promoted by Georgiy Procháska 200 years ago remains disconcertingly alive and well. The mysterious term *soul* has simply been replaced by the equally mysterious term *consciousness* (or *will*). Procházka, Loeb, and Rothwell all indicate in one way or another that voluntary behaviour is essentially conscious (or willful) behaviour, behaviour that is under conscious control, behaviour that the individual perceives him or herself to choose and control.

There are two problems with this position. The first derives from the uncertain status of *consciousness* as a neuroscientific term. Scientists are not supposed to adopt terms simply because introspection suggests them. As Loeb says, "physiologists generally give names when they think, believe or at least hope that those names have a one-to-one relationship with underlying physical structure or at least mechanistic relationships." That is, scientists adopt terms only when they need them to describe

distinct classes of phenomena or relationships between phenomena, and the goal is to have as few terms as possible. To this point, there do not seem to be observable, measurable phenomena that demand the term *consciousness* (e.g. Vanderwolf 1998). That is, there are no experimental observations that cannot be described by much more tractable and limited terms, such as *attention, perception* or *state of alertness*. The term *consciousness* may be useful or even essential in other contexts, in discussions of free will or legal responsibility, for example. But these as currently formulated are not scientific issues, and, thus, their resolution is not within the mandate, or the capacities, of neuroscience. Consciousness is certainly of great interest to the general public, and, thus, neuroscientists must at some point address it in explaining and justifying their work. However, this obligation ought not to impinge on the theoretical framework of the discipline. Because consciousness lacks a well-defined place in neuroscience, it is a weak foundation on which to base the distinction between reflex and voluntary behaviours.

The second problem is that the division of brain function into conscious and unconscious is not derived from the hypothesis that forms the theoretical basis of modern neuroscience. Progress in the early nineteenth century overturned the belief (e.g. Procháska 1784) that the brain has two distinct and disconnected functions, and replaced it with a single comprehensive hypothesis of brain function (Young 1970; Clarke and Jacyna 1987). The most important advance was the discovery by Charles Bell and Francois Magendie that the posterior spinal roots are sensory, conveying input to the brain, while the anterior spinal roots are motor, carrying output to the muscles. Though it may be difficult to fully appreciate at this distance, their discovery had enormous importance. It has been described as the most important physiological discovery since Harvey's description of the circulation of the blood two centuries earlier. The discovery concentrated attention on the brain's role as the interface between sensory input and motor output and, thereby, became the central event in a complex of scientific and philosophical developments that produced a single comprehensive hypothesis of brain function.

This hypothesis is that the entire function of the brain is to convert inputs from its internal and external environments into appropriate outputs, that the brain is an organ that connects stimuli, or activity in sensory nerves, to responses, or activity in motor nerves. The formulation and general acceptance of this *sensorimotor hypothesis* in the first half of the nineteenth century was the beginning of modern neuroscience. It was a scientific revolution, a paradigm shift in the sense defined by Kuhn (1962). Ever since then, the first assumption of neuroscience research has been that complete understanding of the connections between sensory input and motor output would constitute complete understanding of nervous-system function.

With the advent of the sensorimotor hypothesis, the previous meanings of *reflex* and *voluntary*, embodied in

Georgiy Procháska's eighteenth century treatise (and surviving in the current reliance on the conscious/unconscious distinction) became obsolete. Before the nineteenth century, voluntary behaviour was the product of the "rational soul," which, as Procháska said, uses the nervous system as a conduit for producing "its own actions," while reflex behaviour was the product of interactions between the nervous system and its environment that occur "without the consciousness or assistance of the soul." But the sensorimotor hypothesis has no place for the soul and "its own actions," nor for other concepts based solely on introspection. For modern neuroscience, behaviour is the product of sensory input combined with the characteristics and capacities of the nervous system, as determined by genetic endowment and modified by subsequent events (e.g. growth, trauma, ageing). These characteristics and capacities, which include the mechanisms that underlie stereotyped outputs like locomotion, define the substrate of neural structure and activity that connects sensory input to motor output. In this new theoretical frame, behaviours are responses to stimuli, and the difference between voluntary behaviours and reflex behaviours lies in the responsible stimuli.

Defined in terms of the sensorimotor hypothesis, reflex behaviours result from recent stimuli: if recent stimuli are known, reflex behaviours are predictable. For example, a tendon tap usually ensures that muscle contraction will occur a brief and predictable time later. In contrast, voluntary behaviours result from both recent and remote stimuli: they cannot be predicted from recent stimuli alone. Recent stimuli have only a permissive or enabling function. For example, the sudden appearance of an old acquaintance raises the possibility of a greeting, but it does not determine what the greeting will be, or even guarantee that it will occur. The behaviour is a response to an extensive and incompletely defined body of remote stimuli, including the original introduction, later interactions, the numerous experiences that determine a person's characteristic interactions with others (i.e. personality), the experiences with both internal and external environments that affect mood, etc.

If, as the sensorimotor hypothesis implies, a voluntary behaviour is a response to stimuli distributed throughout an individual's previous history, the insight provided by consciousness is nearly worthless, and brings to mind a quotation attributed to the legendary financier J. P. Morgan: "A man has two reasons for everything he does: the reason he gives you and the real reason." The more complex the origins of a behaviour, the less reliable consciousness is likely to be as a guide to those origins.

The reflex/voluntary distinction derived from the sensorimotor hypothesis of neuroscience is not absolute; all behaviours fall on a continuum from purely reflex to purely voluntary, and none is purely one or the other. Even the simplest reflex behaviours, such as the tendon jerk and the vestibuloocular reflex, can be affected by remote stimuli and, thus, are not completely predictable from present circumstances (Miles and Fuller 1974; Wolpaw et al. 1983; Du Lac et al. 1995; Wolpaw 1997).

These reflexes can be operantly conditioned and, to the extent they can be conditioned, they must be considered voluntary behaviours. Conversely, as several earlier sections of this article observe, even the most overtly voluntary behaviours have reflex components (that is, components that do not depend on remote stimuli).

Considerable interest has focused on relatively simple behaviours that are midway between reflex and voluntary. These include so-called long-latency, or transcortical, reflexes (Hammond 1956; Lee and Tatton 1975). Like simpler reflexes, these behaviours are strongly tied to a specific, immediately preceding sensory input. At the same time, they are also determined by a somewhat earlier stimulus, such as the instruction given by the investigator, that establishes behavioural set. They are more voluntary than the simplest reflexes because they depend on the earlier stimulus, and they are more reflexive than other voluntary behaviours because they are responses to a relatively recent and well-defined body of stimuli (i.e. the instruction plus the sensory input that immediately precedes the response) and because some information is available concerning the neuronal mechanisms underlying the influence of the instruction (e.g. Evarts and Tanji 1974; Macefield et al. 1996).

In summary, the nineteenth-century acceptance of the sensorimotor hypothesis that the whole function of the nervous system is to convert sensory input into appropriate motor output, which was the beginning of modern neuroscience, compelled redefinition (or rejection) of many terms originally derived from introspection, including *reflex* and *voluntary*. To return to the quotation (Foster 1895) that was the starting point for the Neural Control of Movement workshop, reflex behaviours are responses to recent stimuli, to which they are linked by relatively "short and simple" neuronal connections, and voluntary behaviours are responses to both recent and remote stimuli, to which they are linked by relatively "long and complex" neuronal connections.

I believe that these are the definitions of *reflex* and *voluntary* that actually operate in neuroscience today. Neuroscientists who say they are studying reflex behaviours are studying behaviours in which the connections from stimulus to response, from experience to behaviour, are known to be, or at least believed to be, short and simple enough to be accessible to description with presently available methods, and they are excluding by one means or another voluntary behaviours, or behaviours involving connections so long and complex as to defy present-day analysis.

Implicit in these definitions (and illustrated in Clarac's section) is the expectation that, as methodology and understanding advance, the class of reflex behaviours will grow larger and larger and the class of voluntary behaviours smaller and smaller. More and more behaviours will become predictable as the mechanisms of their generation from recent and remote stimuli become clear. This prospect, while exciting for neuroscientists as neuroscientists, is disturbing for anyone concerned about issues such as the meaning of legal responsibility for

one's actions. It suggests that the advance of neuroscience, like those of nuclear physics earlier in this century and molecular genetics at present, will have consequences extending far beyond science and medicine.

Conclusions

To no one's surprise, this review, and the workshop preceding it, did not produce agreement on the meaning of the terms *reflex* and *voluntary* in contemporary neuroscience. The five authors approached the issue from different directions, analysed it in different ways and reached different conclusions. Nevertheless, the presentations do in fact permit consolidation into two basic positions: the Prochazka/Loeb/Rothwell position and the Clarac/Wolpaw position.

Prochazka, Loeb, and Rothwell each focus in one way or another on control or consciousness as the crucial distinction between *reflex* and *voluntary*. For Prochazka, voluntary behaviours are those that appear to the person performing them, and to observers, to be chosen or to be suppressible at will, while reflex behaviours are those that appear to be automatic and hard to suppress. For Loeb, voluntary behaviours are those that proceed only under conscious control, while reflex behaviours are those that cannot be modified voluntarily, that is, consciously, during their execution. Rothwell feels that it does not matter whether an ongoing movement is being performed consciously: if we can interrupt it, we can say it is voluntary. All movements then become *automatic* or *reflex*; *voluntary* is simply a measure of how well we can influence them. In contrast, Clarac and Wolpaw focus on behaviours as sensorimotor interactions and see the complexity of the interaction as the crucial distinction between *reflex* and *voluntary*. For Clarac, a reflex is a simple input-output reaction and may be either natural or an experimental tool for exploring the nervous system. For Wolpaw, a reflex is a behaviour produced by a defined input-output pathway, while a voluntary behaviour is produced by a complex, and as yet undefined, input-output pathway.

The Prochazka/Loeb/Rothwell position has the virtue of being congruent with the traditional and lay meanings of *reflex* and *voluntary* and is, therefore, useful for explaining neuroscientific insights to a wider audience. On the other hand, it turns on the meaning of *consciousness* or *will*, and these are difficult terms with as yet uncertain status in neuroscience. The Clarac/Wolpaw position has the virtue of physiological and anatomical clarity, which means that its experimental and theoretical applications are more straightforward. On the other hand, it avoids the issues surrounding consciousness, which are of great formal and informal interest to both scientists and non-scientists.

The choice between these positions will differ from scientist to scientist and with the uses that he or she has for the terms *reflex* and *voluntary*. While the authors of this review have each argued for their own views, their

goal as a group has been to clarify the different ways in which different neuroscientists use these terms. Revealing these differences, and thus encouraging speakers and writers to clarify how they are using the terms, should foster more precise and, thus, more productive communication. It should also highlight the need for careful thought before neuroscientists incorporate these terms in their experimental designs and interpretations.

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