The 'prediction imperative' as the basis for self-awareness

Rodolfo R. Llinás[1,*] and Sisir Roy[2]

[1]*New York University School of Medicine, 530 First Avenue, New York, NY 10016, USA*
[2]*Physics and Applied Mathematics Unit, Indian Statistical Institute, 203 Barrackpore Trunk Road, Kolkata 700 108, India*

Here, we propose that global brain function is geared towards the implementation of intelligent motricity. Motricity is the only possible external manifestation of nervous system function (other than endocrine and exocrine secretion and the control of vascular tone).

The intelligence component of motricity requires, for its successful wheeling, a *prediction imperative* to approximate the consequences of the impending motion.

We address how such predictive function may originate from the dynamic properties of neuronal networks.

Keywords: subjectivity; thalamocortical loop; gamma band; Bayesian statistics

1. INTRODUCTION

While the present set of papers has centred on the general theme of prediction, the realm of such a predictive property can be addressed at many levels. From our perspective, prediction in all its forms is a premotor parameter, which may or may not be enacted. The nervous system evolved such that multicellular creatures that move in a purposeful fashion, i.e. non-randomly, have a clear selective advantage. To accomplish such 'intelligent movement', the nervous system evolved a set of strategic and tactical rules, a key element of such being prediction: the ability to anticipate the outcome of a given action on the basis of incoming sensory stimuli and previously learned experiences or inherited instincts. This ability to predict the outcome of future events is, arguably, the most universal and significant of all global brain functions.

The mechanism of prediction is ubiquitous in the brain's control of movement. Consider the simple act of reaching for a carton of milk in the refrigerator. Without giving much thought to our action, we must predict the carton's weight and the compensatory balance that we must apply for a successfully smooth trajectory of the carton from the refrigerator. Indeed, before even reaching, we have made a ballpark prediction of what will be involved. And surprisingly, we often hit the carton against the top shelf—because it is lighter than we had unconsciously predicted.

Furthermore, we can assume that the prediction in movement must be unique (i.e. the CNS can only operate in a probability space having only a one-dimensional axis), and so, predictive functions must be collapsed to a one-dimensional vector, which will be the base for motor prediction at any given moment. Concerning the proper mathematical format with which to understand the brain decision theory, the

possibility of using Bayesian statistical methodology has raised much interest (Körding 2007). The possibility of using the concept of functional geometry associated with neuronal network properties to understand the predictive properties of brain was initially proposed in the late 1970s and early 1980s (Pellionisz & Llinás 1979, 1985). The spatio-temporal nature and this metric property has been addressed more recently from a dynamic, rather than as a linear connectivity matrix transformation, under the term dynamic geometry, where the metric is considered to be statistical in nature (Roy & Llinás 2008).

The functional basis for such a statistical metric view of internal functional space arose from the experimental finding that inferior olive neurons are endowed with weakly chaotic intrinsic oscillatory properties (Makarenko & Llinás 1998). As with the initial network tensor approach, dynamic geometry transforms dynamic covariant vector (associated with sensory inputs) to contravariant dynamic vector (associated with motor outputs). From this perspective, the distribution associated with the statistical metric predicts the movement uniquely. The application of Bayesian methodology (Körding 2007) to decision making becomes an added attractive avenue. Particularly so, because one of the most significant issues in Bayesian approach concerns the genesis of priors (prior belief or prior knowledge) in neuronal circuits.

2. PREDICTION AND MOVEMENT

Since the ability to predict evolved in tandem with increasingly complex movement strategies, we may address movement control in order to understand prediction. Let us return to the refrigerator for a carton of milk. The appropriate pattern of contractions must be specified for an extension/grasping sequence to be properly executed (add to this the correct use of postural muscles for support of the body while bending forward during the reach). Each muscle provides a

direction of pull (a vector) composed of individual muscle fibres operated in pre-established groups based on their common innervations by given motor neurons. These contractile ensembles are known as motor units (a single motor neuron innervates tens to hundreds of individual muscle fibres). A given muscle may be composed of hundreds of such individual motor units. The number of muscles multiplied by the number of motor units in each muscle may then be viewed as the total number of degrees of freedom for any given movement. A movement such as reaching into the refrigerator is considered a simple one. However, from a functional perspective, even a simple movement often engages most of the body's muscles, resulting in an astronomical number of possible simultaneous and/or sequential muscle contractions and degrees of freedom. In addition, the arm may be brought towards the milk carton from any number of initial positions and postures (maybe your back hurts, so reach from an unusual stance). All of this potential complexity exists before the load is actually placed on your body; you have yet to pick up the carton and can only guess its weight during your initial reaching motion.

So, this simple movement is not simple at all when we break it down and try to understand how the brain handles all of this. However, the dimensionality of the problem of motor control does not derive solely from the number of muscles involved, the differing degrees of pull force and angle, and so forth. The real dimensionality of the problem stems from the complicated interaction between the possible directions of muscular pull and their temporal sequence of activation.

Much of motor control occurs in real time, 'online', as it were. Our movements, from start to finish, are seldom under stimulus-free conditions. Consider the following scenario: riding your bicycle while holding a cup of coffee. The combination of muscle contraction and relaxation at any given moment is often determined as a movement sequence and executed in response to teleceptive stimuli (hearing and vision), kinaesthetic feedback (your feeling of the bicycle and of the cup of coffee) and your intentions (drink your coffee and get to the your destination as soon as possible). It is generally assumed that the optimal controller is one that produces the smoothest possible movements. To minimize the accelerative transients that produce jerkiness in movement, this ideal implies continuous monitoring at a sampling rate of the order of milliseconds or faster (as in the case of your auditory system), as well as feedforward and feedback influences on the selected activation sequences. Yet, we may evaluate quantitatively whether it is computationally possible for the brain to control movement in such a continuous, online manner.

From the heuristic description above, and given that there are 50 or so key muscles in the hand, arm and shoulder, which one uses to reach for the milk carton, over 10^{15} combinations of muscle contractions are possible; this is a staggering number to say the least. If during every millisecond of this reaching/grasping sequence the single best of the 10^{15} combinations is chosen after an evaluation of all of the possibilities, then 10^{18} decisions would have to be made every second. This would relegate the brain, if it were to be a

computer, to being a 1 EHz (1 million GHz) processor when choosing the correct muscle combinations to execute appropriately this relatively simple, reaching/grasping sequence. In reality, even the above scenario is an oversimplification. The dimensionality of the problem of motor control is increased many orders of magnitude when one also considers that there is a bare minimum of 100 motor units for every muscle, and that each muscle pull may, and most likely will, involve differing sets of motor neurons.

The brain does not seem to have evolved to deal with the control of movement in the fashion described above; especially when one considers that there are only approximately 10^{12} neurons in the entire brain. It is, therefore, clear that the continuous control of movement demands an extremely high computational overhead. This is true if the brain is controlling the movement by regulating the activity of every muscle discretely in parallel, or by choosing and implementing combinations of muscles. We do, of course, make complicated movements, and quite often. To delve further into this issue, we must ask the following questions.

(i) How might the dimensionality problem of motor control be reduced without significantly degrading the quality of movement sequences?

(ii) Which aspects of brain function may provide clues to solve this problem?

(a) *The discontinuous nature of movement*

A relatively straightforward approach to reducing the dimensionality of motor control would be to decrease the temporal resolution of the controlling system, i.e. remove it from the burden of being continuously online and processing. This can be accomplished by breaking up the time line of the motor task into a series of smaller units over which the controller must operate. Control would be discontinuous in time and thus the operations of such a system would occur at discrete intervals of a '∂t'. We must consider an important consequence of this approach, namely that the movements controlled by this type of pulsatile system would not be executed continuously in the sense of demonstrating obligatorily smooth kinematics, but rather would be executed in a discontinuous fashion series of muscle twitches that are linked together. Motor physiologists have known this fact for over a century: movements are not executed continuously, but are discontinuous in nature. Indeed, as early as 1886, E.A. Schafer indicated that human movement was discontinuous.

More recently, Valbo & Wessberg (1993) and Wessberg & Valbo (1995) found prominent 8–10 Hz discontinuities in slow and 'smooth' finger movements. They suggested that such discontinuities are most likely generated from the CNS levels above the spinal cord, as the latencies of the stretch reflex were incompatible with the timing of the observed discontinuities of the movements. The stretch reflex is a simple, negative feedback mechanism involving a motor unit and its associated segmental spinal cord circuitry; when a muscle is passively stretched, this compensatory reflex causes a subsequent contraction. The latency of this reflex (from stretch to contraction) has been worked out, and it is

clear that this mechanism cannot explain the timing of the tremor components seen in the above study. Accordingly, Wessberg & Valbo (1995) suggested that the drive causing these periodic components must derive from structures rostral to the spinal cord, i.e. the brain.

We see that the underlying nature of movement is not smooth and continuous as our voluntary movements overtly appear; rather, the execution of movement is a discontinuous series of muscle twitches, the periodicity of which is highly regular. Furthermore, this may be seen as a physiological tremor that is apparent even at rest (when we are not actively making movements). Thus, the tremor is highly associated with movement onset and movement direction. For instance, upward movements are initiated during the ascending phase of physiological tremor (Goodman & Kelso 1983). What do these rhythmic discontinuities represent? What might be their functional significance? To understand this, we may apply Occam's razor.

A parsimonious explanation might take into account the high functional overhead the brain must handle in the control of movement. Rather than an inherent property of muscle itself, this physiological tremor might be an 'echo', at the musculoskeletal level, of a descending command that is pulsatile in nature. If the control system operates discontinuously (to avoid high computational overhead), a pulsatile nature is ideal. While this is a step in the right direction for lowering our functional overhead (as far as control of movement is concerned), there may problems with this pulsatile control. *Discontinuous movements may result in further benefit, beyond lowered computational load.* What else might be gained by pulsatile control through time, apart from easing up on the brain's workload?

(b) *How does the brain predict?*

For the nervous system to predict, it must perform a rapid comparison of the sensory-referred properties of the external world with a separate internal sensorimotor representation of those properties. For the prediction to be usefully realized, the nervous system must then transform into or use this premotor solution in finely timed and executed movements. Once a pattern of neuronal activity acquires internal significance (sensory content gains and internal context), the brain generates a strategy of what to do next, i.e. another pattern of neural activity.

This strategy can be considered an internal representation of what is to come, a *prediction imperative*, in order to become actualized in the external world.

3. MOTOR BINDING IN TIME AND THE CENTRALIZATION OF PREDICTION

First, a pulsatile input into motor neurons from a control system, as opposed to a command system, may prepare a population of independent motor neurons for descending control by uniformly biasing these motor neurons into their linear range of responsivity (Greene 1982). To clarify, a pulsatile control input would serve to 'linearize' a population of highly nonlinear and independent neuronal elements in order to ensure a uniform population response to a control signal. The motor neurons that need to be recruited for a given movement may be, and often are, separated by many spinal levels; this mechanism may serve as a cueing function to synchronize motor neuronal activation.

Second, a pulsatile control system might allow for brief periods of movement acceleration that would provide an inertial break mechanism to overcome frictional forces and the viscosity of muscles (Goodman & Kelso 1983). For example, when we rock a snowbound car, this movement helps to extract it.

Third, a periodic control system may allow for input and output to be bound in time; in other words, this type of control system might enhance the ability of sensory inputs and descending motor command/controls to be integrated within the functioning motor apparatus as a whole.

We now understand that operating continuously online, which we might have thought of as the only way the brain could bring about smoothly executed movements, is simply not possible physiologically. Instead, the brain has relegated the rallying of the motor troops to the control of a pulsatile, discontinuous signal, which is reflected in the musculoskeletal system as physiological tremor. Other than just saving the brain from being computationally overwhelmed, a pulsatile control input also serves to bring the neurons, muscles or limbs closer to a threshold for some action, be it firing, integration or movement. The possible risks of operating discontinuously in time are beautifully minimized by the synchronizing effect this pulsatile signal has on the independent elements of the motor apparatus at all levels. Let us remember the words of Berstein (1967): 'a mutual synchronization through rhythm is doubtless necessary for the motor apparatus as a whole'.

We see that the muscles are often used in combinations. Fixed or hard-wired synergies are not the only rule, and that muscle combinations clearly change dynamically as they must during the execution of a complex movement. If muscle collectives are the unit to be controlled, as opposed to individual muscles, then what does this ask of the central process underlying movement control? It demands that the control system is able to reconfigure itself dynamically so that these collectives are cast temporarily, quickly dissolved and rearranged as required, as a complex movement proceeds. If one agrees that the CNS has many possible solutions for a given motor task, then it follows that any given functional synergy organized by the brain must be a fleeting, dissipative construct. Furthermore, such constructs may not be easily recognized in behaviour as an invariant pattern of muscle activation such as those we recognize in many overt, stereotypical reflexes.

An 'over complete' system of muscle collectives would ensure a degree of versatility and flexibility in choices that the control system could make. If we think of all the different ways we can reach for the milk carton, the idea of over completeness is clear. If the motor control system may select from an over complete pool of similar functional synergies, any number of which gets the job done reasonably well, then this would certainly lower the burden for the control system. It would ease the demand for precision: for having to make the right choice every time.

4. THE OPEN AND CLOSED LOOP DOUBLE DIPPING

The execution of rapid, voluntary movements requires two components with differing forms of operation. The first component is an initial, ballistic approximation of the movement's end point (get your hand close to the carton of milk); the second component fine-tunes the movement using tactile, kinaesthetic, vestibular (balance) or visual feedback (grasp the carton). The first component is performed 'open looped' and in a feedforward manner. The second component operates 'closed looped' meaning that it allows for sensory feedback to refine the movement as it is being executed.

Concerning execution, Greene (1982) suggested that the synergy underlying the feedforward component of a complex voluntary movement is selected from a variety of ballpark estimates that will approximate, but not precisely render, the desired end point. In this scheme, the magnitude of the feedback adjustment of the movement is inversely proportional to the precision with which the feedforward contribution can achieve the desired end point. Selecting a more optimal muscle synergy for the task will reduce the amount of follow-up effort required to correct any deviation produced by the feedforward component. Keep in mind, however, that if only one muscle synergy can approximate the desired movement end point, an erroneous selection would require a large correction with loss of time and movement coordination. But as we mentioned above, since there are many synergies to choose from that will approximate the desired movement, owing to their over completeness, this reduces the necessity for an absolutely precise selection. As long as the selection is within the ballpark, the savings from operating in a feedforward mode will pay for the minimal follow-up effort based on the feedback.

Finally, we come to understand that prediction must be centralized so that the premotor/sensorimotor images formed by the predictive properties are understood as a single construct. This is actually the issue of cognitive binding, and the neural mechanisms that formulate single, cognitively bound constructs are the same as those that generate, as a single construct, the subconscious sensorimotor image that says close your eye, as an object is rapidly approaching.

5. HOW A NEURONAL CIRCUIT CAN PREDICT?

One early attempt to understand prediction (Pellionisz & Llinás 1979) concluded that the brain predicts by taking advantage of the differences in electrical behaviour between the given nerve cells. Because some neurons are highly sensitive to stimuli while others are less so, a ∂t look ahead function might be implemented by neuronal circuits through a process analogous to a mathematical function known as the Taylor series expansion. And so, what is at the heart of such central circuits that could provide the intrinsic drive to generate organized movement if it is not reflex/sensory input? The self-referential approach to the organization of motor control has been given a shot in the arm by the discovery of intrinsic neuronal oscillations and the specific ionic currents necessary for their generation (Llinás 1988). Indeed, oscillatory neuronal behaviour is associated with the generation of an overt, rhythmic activity at 8–12 Hz.

Thus, the periodic activity that is seen in movement is a reflection of a motor control system that operates in a pulsatile, discontinuous-in-time fashion. A control system that synchronizes motor control signals temporally so that movement is executed in an organized, expedient fashion must be centrally located. The spinal cord is more than capable of sustaining a rhythmic movement (Grillner 1985), but it does not have the wherewithal to organize and generate a complex predictive movement.

6. PREDICTION AND 'SELF'

More specifically, while prediction is localized in the CNS, it is a distributed function and does not have a single location within the brain. What is the repository of predictive function? The answer lies in what we call the self, i.e. the self is the centralization of the predictive imperative (Llinás 2002). The self is not born out of the realm of consciousness—only the noticing of it is (i.e. self-awareness). Thus, according to this view, the self can exist without awareness of its existence. That is, even in our case of individuals capable of self-awareness, such awareness is not necessarily present. As an example, consider one's response to fire in one's bedroom. The thought will be 'fire, run!', not, 'fire, I will now run'. Given that prediction may be considered the ultimate and most pervasive of all brain functions, one may ask how this function is grounded such that there evolved only one predictive organ. Intuitively, one can imagine the timing mismatches that would occur if there were more than one set of predictions making judgement calls for a given organism's interaction with the world; it would be most disadvantageous for the head to predict one thing and the tail to predict another! For optimum efficiency, it would seem that prediction must function to provide an unwavering residency and functional connectedness: it must somehow be centralized to the myriad interplays of the brain's strategies of interaction with the external world. We know this centralization of prediction as the abstraction we call the 'self'.

7. DYNAMIC GEOMETRY AND BAYESIAN APPROACH TO DECISION THEORY

If, as stated above, there are 50 or so key muscles in the hand, arm and shoulder that one uses to reach for the milk carton, over 10^{15} combinations of muscle contractions are possible. The choice of appropriate motor command is primarily a decision process. However, in addition to muscular combinatorial issues, noise in the sensory inputs generates uncertainty in the hand's true location. This type of uncertainty possesses the problem of estimating the state of the external world. Bayesian statistics provides a systematic way of approaching such a problem in the presence of uncertainty (Cox 1946; Jaynes 1986; Freedman 1995; Mackay 2003).

In Bayesian statistics, prior knowledge about the system is assumed. The fundamental question regarding the CNS function is the origin of such prior knowledge, and the answer is simple: the morphofunctional brain network, initially inherited and then honed by use. In fact, the origin of a Bayesian framework can be traced to Helmholtz's (1867) idea of perception. It was Helmholtz who realized that retinal images are ambiguous and prior knowledge is necessary to account for

visual perception. Recently, the genetic component has been thought to play a significant role in the development of human depth perception (Yonas 2003). And so, how is prior information encoded in the CNS?

A central question concerning present-day neuroscience is that of understanding the rules for the embedding of 'universals' into intrinsic functional space. Some suggestions have been offered concerning the nature of this CNS internal space that we think addresses this point (Roy & Llinás 2008). The arguments go as follows: if functional space is endowed with stochastic metric tensor properties, then there will be a dynamic correspondence between the events in the external world and their specification in the internal space. We shall call this dynamic geometry because the minimal perceptual time resolution of the brain (10–15 ms), associated with 40 Hz oscillations of neurons and their network dynamics, is considered to be responsible for recognizing external events and generating the concept of simultaneity (Joliot *et al*. 1994).

Essentially, this dynamic geometry helps us understand the nature of sensory–motor transformation. The stochastic metric tensor in dynamic geometry can be written as function of four space–time coordinates (i.e. three space and one time of Minkowski space) and a fifth dimension (Roy 1998). This fifth dimension is a probability space as well as a metric space. This extra dimension is an embedded degree of freedom and is random in nature. In fact, the dynamic geometry framework makes it possible to distinguish one individual from another. The uniqueness of individuals must operate in detail not in principle, i.e. general solutions must operate on the basis of a generalized solution field. Considering the stochastic nature of specific brain function among individuals, they will have both anatomical and functional variances, similar to the differences in their facial characteristics. The variances must be such that they modulate, rather than destroy, the general solution. However, the variances may be so extreme that they negate the function or may even be lethal. Within this framework, social variance enriches the system, as variances augment some properties and diminish others and so individuality is important. Thus, the geometric structure is embedded in the CNS from birth and functional states of neurons are associated with this geometric structure. In this framework, the covariant to contravariant transformation occurs with a certain probability distribution.

Physiological tremor is ultimately the reflection of T-type calcium channel kinetics in inferior olive neurons (Llinás *et al*. 2004) resulting in the fluctuating nature of the geometry of the internal space. Here, the input–output feedback is not simply sequential but related to the stochastic process in equilibrium whose distribution is associated with the distribution of stochastic metric tensor. This gives rise to an optimal (and organized) motor movement. In this situation, Bayesian methodology helps to understand the motor and predictive ability of brains.

This is basically an issue in statistical inference, which can be viewed as information processing relating input and output information. The statistical inference has been studied in various topics in statistics, physics, biology and econometrics. Briefly speaking, inference is

a form of information processing where a black box endowed with prior information (morphofunctional properties) receives input information and sends outputs in the form of parameter estimates and predictive distributions. Bayes' theorem has been widely studied as a model to transform *a priori* information into future inference. In fact, the Helmholtz idea of perception (1867) as 'unconscious inference' is considered as the origin of Bayes' framework. Bayes' theorem is used to calculate the inference distribution in the following manner: given a prior distribution say a Gaussian distribution $p(x)$ and noisy observation o (data), which leads to a Gaussian likelihood $p(o|x)$, then the p inference distribution $p(x|o)$ is given by

$$p(x \mid o) = p(o \mid x)p(x)/p(o).$$

Körding (2007) developed a Bayesian approach, which leads to a better estimate of the possible outcomes than other estimates using sensory input. Recently, Bhattacharya *et al*. (2007) developed a Bayesian methodology to fit the data observed in an underlying process in equilibrium. This methodology can be described as f (data|process, parameters) $\times f$ (process| parameters) $\times f$(parameters). In a formal language, it can be represented as

$$f(Y \mid X, \theta)f(X \mid \theta)f(\theta),$$

where Y is the (set of) observed data; θ is a set of model parameters; and X is an unobserved (latent) stationary stochastic process. This stochastic process is induced by the first-order transition model

$$f(X(t+1) \mid X(t), \theta),$$

where $X(t)$ denotes the state of the process at time t. It is to be noted that given θ, the transition model

$$f(X(t+1) \mid X(t), \theta)$$

is known, but the distribution of the stochastic process in equilibrium, i.e. $f(X|\theta)$, is generally unknown. Here, it is important to note that the data Y has been assumed to be observed when the underlying process is in equilibrium. They called it as latent equilibrium process (LEP). In the next step, Bhattacharya *et al*. developed a methodology to fit LEP within the Bayesian framework. This type of fitting is usually done via Markov chain Monte Carlo (MCMC). It is demonstrated by these authors that this kind of fitting is far from straightforward. They developed a different methodology so as to implement this kind of situation.

Intuitively, we can understand the main idea as follows. Let

$$X_n; n = 1\ldots \ldots N,$$

be a Markov chain where the transition $[X_n|X_{n-1}]$ is known but the equilibrium distribution of X_n is unknown. Under certain conditions, X_n converges to a unique stationary distribution with unknown form, and thus the system develops an estimation inference within the Bayesian framework.

It is possible to show that this convergence to equilibrium distribution happens after a time period known as convergence time. Here, it is assumed that equilibrium is defined dynamically as the result of transitions arising under f (process state at time $t+1|$

process state at time t, parameters) with t as the time period or generation. For infinitely large N, the convergence occurs irrespective of the convergence time. There is an important difference with this approach and a dynamic model where input continuously addressed dynamically in time. Here, input is collected only when the underlying latent stochastic process is in equilibrium.

In the case of decision making by the brain, the underlying feedback process can be thought of as a stationary stochastic process owing to the presence of noise in the sensory input. It needs a small time period (owing to its discrete nature) to reach an equilibrium. This is the convergence time mentioned above. However, in the case of infinitely large N, the equilibrium will be reached, irrespective of this convergence time, and the movements may be considered as continuous.

8. CONCLUSIONS

This paper offers a view of global brain function based on the assumption that the evolution of the CNS is basically geared to optimize prediction in order to generate intelligent motricity. That is, such an intelligent movement is central for ultimate survival; the clearest examples being the fight or flight, and the predatory behaviour, by forms endowed with a brain. By contrast, in those macroscopic living systems where fast displacement is fundamentally non-existent compared with that of animals, such as plants, survival depends on molecular a *priori* defences (biochemical defences bad taste, bad odour, etc.) or static macroscopic entities, such as thorns. Interestingly, the genetic load of plants has a very large defensive component (Manners 2007). Ultimately, as they cannot run away from danger, being a fortress is their only available solution.

Concerning prediction beyond the motor execution realm, it is evident that separating sensory from motor transformations is in the eye of the beholder. Such issues remind us of the discussions between the neurologists and psychiatrists wanting to divide the functional properties of the central nervous system into psychic and neurological functions. That the integration time for the cognition is shorter than that for the motor is well recognized. Most vertebrate forms integrate sensory input at close to gamma band frequency (40 Hz) (Singer 1999; Llinás & Steriade (2006) see also invertebrates Stopher *et al*. (1997)), but they move, as addressed above, at 10 Hz. The advantage of having a more rapid time constant for sensory input is obvious when one considers that the motor execution is irreversible once triggered, as testified by the rules of engagement in most sports (hit or miss). And so, planning/prediction must occur at a faster speed than movement execution if the possibility of corollary discharge (efference copy) is to play a role in such an event (Jeannerod 1997). Indeed, in order to do so, an internal 'forward model' (Wolpert 1997) is required to express the causal relationship between the motor event and the sensory input that triggers it in the context of the expected outcome. Such a relationship was noted in early psychophysical studies (Sperry 1950) and substantiates the view that there is but one fundamental predictive function for sensory–motor transformations.

REFERENCES

Berstein, N. A. 1967 *The coordination and regulation of movement.* Oxford, UK: Pergamon Press.

Bhattacharya, S., Gelfand, A. E. & Holsinger, K. E. 2007 Model fitting and inference under latent equilibrium processes. *Stat. Comput.* **17**, 193–208. (doi:10.1007/s11222-006-9015-6)

Cox, R. T. 1946 Probability, frequency and reasonable expectation. *Am. J. Phys.* **17**, 1–13. (doi:10.1119/1.1990764)

Freedman, D. A. 1995 Some issues in the foundation of statistics. *Found. Sci.* **1**, 19–83.

Goodman, D. & Kelso, J. A. 1983 Exploring the functional significance of physiological tremor: a biospectroscopic approach. *Exp. Brain Res.* **49**, 419–431. (doi:10.1007/BF00238783)

Greene, P. H. 1982 Why it is easy to control your arms? *J. Motor Behav.* **14**, 260–286.

Grillner, S. 1985 Neurobiological bases of rhythmic motor acts in vertebrates. *Science* **228**, 143–149. (doi:10.1126/science.3975635)

Helmholtz, H. 1867 Handbuch der physiologischen Optik (transl. in English by J. P. C. Southhall as Treatise on Physiological Optics). Leipzig, Germany: L.Voss.

Jaynes, E. T. 1986 *Bayesian methods: general background.* Cambridge, UK: Cambridge University Press.

Jeannerod, M. 1997 *The cognitive neuropsychology of action.* Cambridge, UK: Cambridge University Press.

Joliot, J. M., Ribary, U. & Llinás, R. 1994 Neuromagnetic coherent oscillatory activity in the vicinity of 40-Hz coexists with cognitive temporal binding in the human brain. *Proc. Natl Acad. Sci. USA* **91**, 11 748–11 751. (doi:10.1073/pnas.91.24.11748)

Körding, K. 2007 Decision theory: what 'should' the nervous system do? *Science* **318**, 606–610. (doi:10.1126/science.1142998)

Llinás, R. R. 1988 Intrinsic electrophysiological properties of mammalian neurons: insights into central nervous system function. *Science* **242**, 1654–1664. (doi:10.1126/science.3059497)

Llinás, R. R. 2002 *I of the vortex: from neurons to self.* Cambridge, MA: MIT Press.

Llinás, R. R. & Steriade, M. 2006 Bursting of thalamic neurons and states of vigilance. *J. Neurophysiol.* **95**, 3297–3308. (doi:10.1152/jn.00166.2006)

Llinás, R., Leznik, E. & Makarenko, V. 2004 The Olivo-cerebellar circit as a universal motor control system. *IEE J.* **29**, 631–639.

Mackay, D. J. C. 2003 *Information theory, inference and learning algorithms.* Cambridge, UK: Cambridge University Press.

Makarenko, V. & Llinás, R. 1998 Experimentally determined chaotic phase synchronization in a neuronal system. *Proc. Natl Acad. Sci. USA* **95**, 15 747–15 752. (doi:10.1073/pnas.95.26.15747)

Manners, J. M. 2007 Hidden weapons of microbial destruction in plant genomes. *Genome Biol.* **8**, 1–4. (doi:10.1186/gb-2007-8-9-225)

Pellionisz, A. & Llinás, R. 1979 Brain modeling by tensor network theory and computer simulation. The cerebellum: distributed processor for predictive coordination. *Neuroscience* **4**, 323–348. (doi:10.1016/0306-4522(79)90097-6)

Pellionisz, A. & Llinás, R. 1985 Tensor network theory of the metaorganization of functional geometries in the CNS. *Neuroscience* **16**, 245–273. (doi:10.1016/0306-4522(85)90001-6)

Roy, S. 1998 *Statistical geometry and applications to microphysics and cosmology.* Dordrecht, The Netherlands: Kluwer Academic Publishers.

Roy, S. & Llinás, R. 2008 *Dynamic geometry, brain function modeling, and consciousness* (eds R. Banerjee & B. K. Chakrabarti), *Prog. Brain Res.* **168**, 133–144. (doi:10.1016/S0079-6123(07)68011-x)

Schafer, E. A. 1886 On the rhythm of muscular response to volitional impulses in man. *J. Physiol.* (*Lond.*) **7**, 111–117.

Singer, W. 1999 Neuronal synchrony: a versatile code for the definition of relations? *Neuron* **24**, 49–55. (doi:10.1016/S0896-6273(00)80821-1)

Sperry, R. W. 1950 Neural basis of the spontaneous optokinetic response produced by visual inversion. *J. Comp. Physiol. Psychol.* **43**, 482–489. (doi:10.1037/h0055479)

Stopher, M., Bhagavan, S., Smith, L. H. & Laurent, G. 1997 Impaired odour discrimination on desynchronization of odor-encoding neural responses. *Nature* **390**, 70–74. (doi:10.1038/36335)

Vallbo, A. B. & Wessberg, J. 1993 Organization of motor output in slow finger movements in man. *J. Physiol.* (*Lond.*) **469**, 673–691.

Wessberg, J. & Vallbo, A. B. 1995 Human muscle spindle afferent activity in relation to visual and control in precision finger movements. *J. Physiol.* (*Lond.*) **482**, 225–233.

Wolpert, D. M. 1997 Computational approaches to motor control. *Trends Cogn. Sci.* **1**, 209–216. (doi:10.1016/S1364-6613(97)01070-X)

Yonas, A. 2003 Development of space perception. In *Encyclopedia of cognitive science* (ed. R. Anand), pp. 96–100. London, UK: Macmillan.