

Complexity in Neurobiology: Perspectives From the Study of Noise in Human Motor Systems

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ABSTRACT: This article serves as an introduction to the themed special issue on “Complex Systems in Neurobiology.”

The study of complexity in neurobiology has been sensitive to the stochastic processes that dominate the micro-level architecture of neurobiological systems and the deterministic processes that govern the macroscopic behavior of these systems. A large body of research has traversed these scales of interest, seeking to determine how noise at one spatial or temporal scale influences the activity of the system at another scale. In introducing this special issue, we pay special attention to the history of inquiry in complex systems and why scientists have tended to favor linear, causally driven, reductionist approaches in Neurobiology. We follow this with an elaboration of how an alternative approach might be formulated. To illustrate our position on how the sciences of complexity and the study of noise can inform neurobiology, we use three systematic examples from the study of human motor control and learning: 1) phase transitions in bimanual coordination; 2) balance, intermittency, and discontinuous control; and 3) sensorimotor synchronization and timing. Using these examples and showing that noise is adaptively utilized by the nervous system, we make the case for the studying complexity with a perspective of understanding the macroscopic stability in biological systems by focusing on component processes at extended spatial and temporal scales. This special issue continues this theme with contributions in topics as diverse as neural network models, physical biology, motor learning, and statistical physics.

KEY WORDS: Complexity, coordination, sensorimotor noise, timing

I. INTRODUCTION

From the molecules that come together to shape a morning’s cappuccino to the receptors on the tongue that allows one to taste it and the motor system that orchestrates how to reach for and drink it, complexity is everywhere. The human brain, with more than one hundred billion neurons and trillions of synapses, is one of the most complex of known complex systems. The number of possible states of such a system, with its vast network of interconnected circuits, is possibly larger than the number of fundamental particles estimated to exist in the Universe.¹

While there is wide consensus on the fact that the human brain is a complicated system, the use of the term “complex” to describe neurobiology has a definite purpose. To label something a complex system, an implicit requirement is that its components, when acting as a whole, behave in a manner that is

not predictable from the behavior of the individual parts. Often such a system shows collective properties that are unrecognizable from the properties of the component parts. The human brain is such a complex system; it functions collectively in a manner that is quite different from that of a single neuron.

The complexity of the human nervous system can be studied by analyzing multiple levels: 1) the awesomeness of its massive structure and the interconnectedness of the networks therein, 2) how these structures change as the system learns and develops, and/or 3) the computations that it performs across spatial and temporal scales that allow the system to introspect, evaluate, and monitor itself and the various functions of which it is capable. Although each level of analysis is unlikely to provide a unified picture of how the system functions in its entirety, how these levels interact with each other in the presence

of noise and uncertainty is a very promising topic of interest.²

The last couple of decades have seen an explosion in the development of the neurobiological sciences, especially with the advent of neuroimaging technologies. While much has been learned about mapping some cognitive activities specific to pieces of anatomy, this approach has not provided the field with an understanding of how brain networks function as a whole.³ Here we propose a heterodox way of studying human neurobiology and cognition, by taking an approach that pays attention to some the details of neural and behavioral organization commonly overlooked by many neurobiologists, cognitive neuroscientists, and psychologists. In this review, which serves as an introduction to this volume on the sciences of neurobiological complexity, we identify several key areas of emerging activity in human motor control that hold a great deal of promise in our functional understanding of the human brain and the cognitive functions that it supports.

In the first section of this review, we provide an overview for the sciences of complexity as relevant to neurobiology. Following this, we present a summary of advances from the literature and from our own work on the structure of neurobiological noise that has dealt with possible ways to approach the study of the macroscopic organization of the brain and cognitive systems. It is important to keep in mind that this review is an “impressionistic” overview from the perspective of cognitive scientists studying aspects of human perception and action. That said, we use this level of analysis to examine complexity in neurobiological systems at large.

A. Complexity: An Historically Overlooked Topic

Some aspects of scientific inquiry have remained strangely disregarded in the development of research, neglected because scientists consider them to be out of the reach of traditional scientific inquiry. For instance, the behaviorist approach at the beginning of the 20th century considered psycho-

logical processes to be inaccessible by an objective and positivist approach and focused instead on stimulus–response relationships. Particular interactions between levels (behavior and the underlying system that supports it) were neglected because they were of little interest, particularly for promoting a reductionist understanding of biology.

Such was the case for the systematic study of noise and variability, which had been conceived as reflecting unexpected and functionally meaningless phenomena or errors. Researchers thus generally decided to eliminate variability by means of averaging or smoothing, focusing, rather, on mean values or trends supposed to reveal the “true” functioning of the system under study.

Although we could classify complexity as a less-studied science, a number of theoretical ideas about complexity had been developed as early as the middle of the last century. One can cite the pioneer work of Ashby, published in 1947, introducing the concepts of self-organization and emergence, the development of fractal geometry by Mandelbrot, and the later important contribution of Varela, who proposed the concept of autopoiesis to define and explain the nature of complex living systems.^{4–6} In the same vein, Kauffman showed that self-organization could challenge the Darwinian conceptions about evolution; Bak suggested the role that self-organized criticality could play in the maintenance of physical and living systems; and Morin proposed a deep renewal of scientific thought based on a fuller consideration of complexity.^{7–9}

These approaches to complexity have strongly challenged traditional theories, especially those that attempted to account for macroscopic phenomena using linear systems. For example, Ashby (1956) formulated the famous *law of requisite variety*, which challenges the concept of control of complex systems.¹⁰ Following Ashby’s terminology, variety represents the amount of different states that can be observed for a given system. Ashby’s law states that to have system A controlling system B, it is necessary that the variety of the former is greater than (or at least equal to) the variety of the latter. In other words, the controller should be at least as complex as the system it is supposed to

control. Bernstein, one of the pioneers in the field of motor control and motor learning, formulated similar problem in terms of system redundancy: the motor system possesses an abundance of degrees of freedom, whose control seems out of range of an external instance.¹¹ Despite these caveats, a number of theoretical accounts for motor control have supposed this kind of external control using internal representations and computational processes such as motor programs.^{12,13}

The reasons for such persistent reluctance of the scientific community toward complexity are several. The appeal of simple models and linear causalities has obviously played a significant role. The most famous laws that developed during the 20th century, which had a strong impact on the development on psychological sciences, were commonly formulated as very simple generalizations, expressing a continuous and linear relationship between stimulus and response, stimulus and sensation, etc. The list of such relationships includes, among others, Fitts's law describing a linear relationship between movement time and task difficulty, Fechner's law stating that subjective sensation is proportional to the logarithm of stimulus intensity, or the Yerkes-Dodson function relating performance to activation.¹⁴

A second reason for the relative resistance to complexity is the fact that many scientists aim to explain, theorize, and model the systems they study, and they often aim to provide indications about how to control these systems and to predict their future behavior. However, one of the major acknowledged shortcomings of complexity theories is that it is impossible to capture a complex system and its dynamics in a comprehensive model.¹⁵ It has also been suggested that complex systems cannot be entirely controlled and that their long-term behavior remains less than predictable. It is conceivable that such statements promote reluctance among researchers to deal with complexity. Taking complexity into account leads to a deep questioning of traditional models and theories and supposes a real paradigm shift, in the Kuhnian sense.¹⁶

Another factor of resistance has emerged from a possible misinterpretation of the true meaning

of complexity. Weaver (1948) addressed, at least intuitively, this problem by introducing a distinction between *disorganized complexity* and *organized complexity*.⁷ Disorganized complexity refers to systems in which interactions between components are essentially random. In such systems, components are independent, and one can hardly expect to observe any coordinated macroscopic activity. Organized complexity, in contrast, is characterized by correlated interactions between components. These nonrandom relationships provide the system with a coordinated structure, allowing the emergence of macroscopic properties. This is similar to a distinction introduced between complicated and complex systems by Morin.⁹ Complexity has been often conceived in the first sense, as a kind of unpredictable disorder, out of the reach of mainstream scientific inquiry, something mystical. The more recent approaches have adopted a more interesting conception, closer to the concept of organized complexity proposed by Weaver.¹⁷ The general idea that we promote in this article is that complexity that emerges from softly assembled, multilevel coordination among the multiple elements that compose the system leads to metastability and pervasive $1/f$ -type phenomena.¹⁸⁻²²

B. Dynamical Systems Theory and Dynamical Approaches to Neurobiology

An important step in taking into account complexity in biological systems has been the development of the dynamic systems theory, and especially the dynamical approach to cognition that resulted from the systematic study of human coordination.¹⁹⁻²¹ The aim of this approach has been to deal with the dynamics of the macroscopic behavior of complex systems. An important development that has emerged from this approach is the idea that the interplay of the multiple components that comprise the system results in the emergence of a limited set of preferred macroscopic behavioral solutions, called attractors. As such, a complex system can exhibit rather simple and predictable behavior, and researchers can envisage and determine the equations of motion capturing these macroscopic be-

havioral dynamics.²¹

Complexity plays another important role in behavioral dynamics. Complex systems work rather well in the presence of inherent, random fluctuations, and this background noise is essential in the global dynamics of the system. Random perturbations facilitate the exploration of the state space and increase the opportunities for reaching attractive behavioral solutions.²¹ Thus, background noise plays an essential transition role between qualitatively different regimes of functioning, as it allows moving the system from less attractive modal regions of the state space toward more attractive regions. As such, equations of motion based on dynamic systems theory take the form of systems of stochastic differential equations, including a deterministic part, which accounts for the qualitative structure of the state space, and a stochastic component that generates the dynamics of behavior within this state space.

However, if complexity is conceived as a necessary condition for the emergence of macroscopic behavior, it essentially remains a background assumption. The question is more “What emerges from complexity?” than “How does it emerge from complexity?”

In this respect, contemporary approaches to complexity in neurobiology adopt a rather innovative point of view. An important development that has facilitated overcoming previous resistances is the discovery of a possible link between the correlation structure of the time series produced by a system and its complexity properties, such as its metastability.²² More precisely, a number of authors have postulated that the presence of long-range correlations in successive measurements, performed on a given system in steady-state condition, could reflect properties of its functional organization, assessed on a continuum between complete disorder and strict order.^{18,22–24} Moreover, evidence has accumulated which shows that this specific correlation pattern of fluctuation in any bio-behavioral variable is typical of the performance of healthy and perennial systems, while being altered with age or disease, either in the direction of excessive order, or disorder.^{25,26} These observations have led

to a coherent and innovative framework that links the notions of complexity, health, and adaptability, and that also considers aging and disease to be related to a loss of systems complexity.^{25,27}

During the last two decades, a growing interest in nonlinear time series analysis has emerged in a number of scientific domains and has yielded to the discovery of long-range correlations, or $1/f$ fluctuations, in most living systems.²⁸ These results were first considered a mathematical curiosity, a ubiquitous phenomenon without much scientific interest. Progressively, however, considerable efforts have been made to overcome this initial assessment and to investigate in depth the origins and the meaning of these fluctuation patterns. The aim of most recent research in this domain is to exploit behavioral measures for exploring the intimacy of a system, and more precisely, to obtain a better understanding of the principles that underlie this “optimal complexity” between order and disorder. This approach, which consists of inferring information about the internal organization and functioning of the system from the statistical properties of its outcome variables, represents an exciting challenge.²⁹

In the following sections, we highlight briefly what we think to be some of the most exciting developments in complex systems approaches to neurobiology, in addition to the other excellent papers published in this volume.

C. Noise in the Nervous System

Even outside of scientific communities studying statistical mechanical processes in biology, the study of noise has emerged as an important component in a wide range of neurobiological systems. In their seminal paper, Faisal et al. (2008) looked at the presence of noise in the human nervous system across multiple modalities and scales (spatial and temporal).²

In Figure 1 (reproduced with permission from Faisal et al., 2008), the authors illustrate the presence of noise at almost every possible level of operation in the nervous system during the exemplar task of catching a ball. Whereas we as scientists have often been sensitive to noise at the sensorimo-

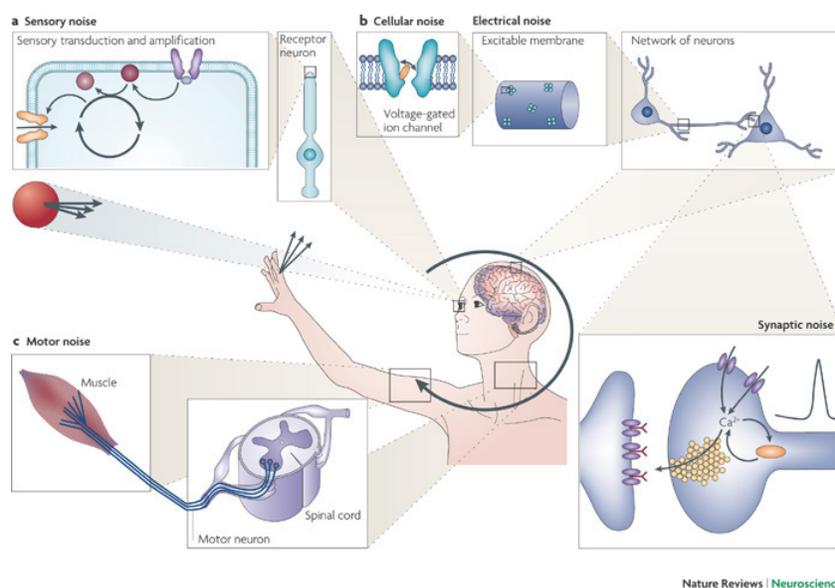


FIGURE 1: A depiction of noise at multiple levels on the nervous system. A fundamental question we examine in this paper is how the nervous system exploits noise at all levels. We have provided examples of how the sciences of complexity provide a unique window into understanding how noise can be used the control of human sensorimotor processes. [Figure reproduced with permission from Faisal et al. (2008) Noise in the nervous system. *Nat Rev Neuro* 9(4):292–303 ©Nature Publishing Group].

tor level, there has been little interest in relating this to noise at lower levels in the nervous system, for example, at the level of ion channels of excitable membranes or synaptic transmission or network interactions. In the approach they pioneered, Faisal et al.² suggest that the way the central nervous system (CNS) deals with noise and uncertainty shows similarities across all these distributed spatial and temporal levels. Following this idea, we suggest that variability and uncertainty at the cellular level would be incomplete without a complementary analysis of the macroscopic functions that these assemblies support. The most attractive feature of the approach we suggest is the idea that noise that is present at the cellular and molecular level influences human macroscopic functions related to perception and action. Therefore, we should be able to make experimental predictions on the basis of noise at each level for phenomena observed at other levels of analysis.

Consider, for example, the task that is present-

ed in Figure 1. While moving our arms to catch a ball, we are dealing with noise at all the aforementioned levels. The motor commands issued to move the arm are corrupted by noise, much like the sensory system that estimates the position of the arm and the ball. Successful execution of the task of catching requires the use of optimal feedback control of task-relevant parameters. This is achieved by allowing the variation of parameters that do not affect the task.^{30,31}

In a recent paper from our group, we demonstrated that variation in joints during a stick-balancing task allowed variation with the control-space that was not relevant to the task, while maintaining tight control of the parameters that led to successful performance.³¹ The general emerging story from this line of work is that the CNS actively manages noise during what appears to be deterministic control of human movement.

To fully understand the control strategies used by the CNS, we need to establish methods that

distinguish purposeful variability from noise. The stochastic optimal feedback control models^{29,31} have been very successful at promoting the idea that the CNS works well in the presence of fluctuations. However, noise has always been treated in these models as random variation that does not have structure. It would be interesting to test models of motor control that suggest optimization in the presence of signal-dependent noise² with the employment of correlated noise (of various kinds) commonly found in neurobiological systems.

D. Structure of Noise in the Context of Steady-State and Behavioral Transitions

In the previous section, we saw that the CNS packages noise resourcefully in the successful performance of goal directed tasks. An alternative approach that we have pioneered is the idea that noise in the form of local variance (as posited by Faisal et al.²) and long-range correlations can be mutually adjusted resourcefully to stabilize and adapt behavior to particular contexts.³²

The variability of any given system can be decomposed into two independent parts: local variance (LV) and serial correlation (SC) structure. We predicted that a co-adjustment of these two determinants of variability constitutes a resource for adaptive systems. This resource can be adapted for differential use during steady-state behavior and under critical conditions of phase transition and instability. To test this hypothesis, we used the very popular bimanual coordination paradigm introduced by Kelso.²⁰ In this experimental paradigm, human participants typically produce oscillations of the hands (or other effectors) in-phase (relative phase between limbs 0°) or anti-phase (spatial opposite patterns, relative phase at 180°).

Participants performed bimanual oscillations in four tasks: 1) in phase at comfortable frequency (IP-COMF), 2) in phase at critical frequency (IP-CRIT), 3) anti-phase at comfortable frequency (AP-COMF), and 4) anti-phase at critical frequency (AP-CRIT). The critical frequencies were determined for each individual through an earlier experiment in which they were forced to make phase

transitions from anti-phase to in-phase patterns by systematically increasing the movement frequency. The correlations between the local variance and the serial long-range correlations observed between cycles at steady-state and critical frequencies is shown in Figure 2.

In Figure 2, we represent the landscape that depicts the stability well for in- and anti-phase coordination in the form of a potential function.³³ A quick glance at the correlations between local variance and serial correlation shows that this value increases gradually as the depth of the attractor decreases. In other words, there is a much larger correlation between LV and SC in the anti-phase coordination conditions, when the intrinsic stability of the coordination decreases. The correlation becomes significant in the critical condition when there is actually a risk of spontaneous phase transition.

In this study, if we had focused exclusively on LV or SC, we would have an incomplete picture of the system and its propensity for stability and adaptability. Without looking at the interplay between SC and LV, we might have concluded that the evolution of long-range correlations had no effect on the critical condition of performance. Thus, by relating LV and SC we have shown that noise is a resource that can be adjusted for system stability and adaptability. By packaging one form of noise optimally at the cost of another, the CNS might make itself stable and adaptable at the same time. As neurobiologists studying such systems, we might conclude that decomposing variability into LV and SC is a useful way to disambiguate the complex relationships among variability, stability, and adaptability.

The major difference between the approach outlined here and the one by Faisal et al.² from the previous section is that we have shown that noise is not a structural limitation to be overcome but rather a resource that the CNS exploits for functional stability.

E. Complexity and Learning Dynamics as Changes in Statistical Distributions

An exciting new development in complex systems—

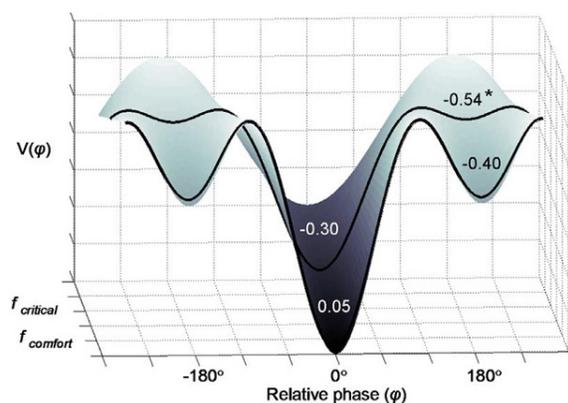


FIGURE 2: Coefficients of linear correlation between the local variances and mean Hurst exponents of relative phase obtained in the four experimental conditions: IP-COMF, IP-CRIT, AP-COMF, and AP-CRIT. The coefficients are shown against the graphical representation of the potential function,³³ which formalizes the stability regimes of bimanual coordination dynamics as a function of required relative phase and oscillation frequency. [Reproduced with permission from Torre & Balasubramaniam, 2011. ©American Psychological Association.]

based approaches to the study of movement systems is the characterization of behavior in terms of statistical distributions. About a century ago, soon after the discovery of the central limit theorem, a number of studies started reporting regressions to the mean. Now statistical tests based on the normal distribution are ubiquitous in almost every field of science. However, not all distributions observed in nature are Gaussian, a common assumption made in several seminal studies that characterize noise in neurobiological systems.²

The discovery of power laws (e.g., between frequency of an event to some other aspect of the event, like its size) such as Zipf's law is becoming more common in the neurobiological sciences.¹⁸ Another statistical distribution that is also now being observed across various spatial and temporal levels of analysis is the Lévy distribution.^{34,35} Unlike Gaussians, Lévy distributions have infinitely long tails, so the probability of finding a data point in the distribution does not exponentially diminish

as one reaches the tail of the distribution.

In a recent study of free recall in memory, it was shown that retrievals decline as recall progresses, but the time intervals between retrievals showed Lévy-distributed dynamics.³⁴ Lévy flight distributions, characteristic of foraging behavior, may thus underlie retrieval in semantic memory. The simple modification of not considering these distributions as Gaussian led to a path-breaking discovery that enabled us to relate the ecology of foraging behavior, search, and retrieval in memory. In a recent series of studies from our group, we discovered Lévy-distributed dynamics in human stick balancing.³⁵

During human stick balancing, we observe heavy-tailed distributions with incremental changes in fingertip speed that conform to Lévy-distributed probability density. When balancing a stick, actors usually make a combination of small and large displacements. When we had subjects practice this task and gain proficiency at stick balancing, the probability of finding large displacements increased. This corresponded to more variable yet more stable performance. Thus, learning made the actors more tolerant of larger displacements in performance. Additionally, the average duration between corrective displacements also increased with learning.³⁶ This suggests that the neural control process was discontinuous, supporting existing evidence that power-law scaling occurs in the frequency domain. Corrective displacements occur at all time scales of activity, but they are more likely to happen for displacements that are shorter than neural latencies.³⁷ Although this result might seem paradoxical, it elucidates the limitations of existing models that equate performance with constrained variability. The stabilizing effect of short-time-scale stochastic processes in balancing³⁸ is further highlighted here.

In summary, the central message from this line of work is that equating noise to simple Gaussian processes would not have allowed for the detection of these stochastic processes that work at time scales faster than neural delay. In the future, a more sophisticated understanding of these processes will provide a more accurate understanding

of how learning changes both cognitive and motor performance.

F. Individual Differences Through the Study of Complexity: Event vs. Emergent Timing

An important problem that has remained out of reach for many neurobiologists and psychologists is the one of understanding where individual differences come from. Although there is significant variability in the performance of a motor task by the same individual in two trials, no two individuals are ever alike.³⁹ Of course, this can be attributed to the vicissitudes of individual experiences, initial conditions, boundary conditions, and structural differences in the components that make up the two biological systems. Thus, the question of how one might compare these two complex systems with much in common is a very important one, but it is also a question for which there are no obvious answers.

To pursue this issue, we sought to look at a motor task at which individuals might differ greatly. For many years, it had been assumed that humans possess a general-purpose timing capability. This implies that someone with good sensorimotor timing skills at drawing would be a good piano player and would also be very good at timing a golf putt. The basic theory is that a common clock-like mechanism underlies the timing of all actions and is effector neutral. Thus, our ability to speak or run faster or slower is governed by the same timekeeper mechanism.

However, studies by Zelaznik et al.⁴⁰ showed that this was not the case. In particular, they showed that people who are good at finger tapping were not particularly good at circle drawing and vice versa. Stated differently, the timing errors made when performing a certain timing task do not predict performance on a different sensorimotor timing task. This result was later corroborated by neuropsychological evidence that showed that patients with cerebellar damage⁴¹ exhibited high timing errors and variability in finger tapping, but did not demonstrate this high variability and interval error

while drawing circles. It has been assumed that the cerebellum (the locus of time representations in the brain) would govern the timing processes for all timed actions. The results of Spencer et al. have challenged this fundamental assumption.⁴¹ These authors have further suggested that “event” timing, under the control of cerebellar processes, requires the existence of a discrete event defining the timing task. In other words, tasks with specific temporal goals were the only one that recruited cerebellar resources. Tasks for which timing emerges from the movement of the effectors do not use cerebellar resources. In the latter case, the regime of timing is an “emergent” property of the human sensorimotor system and its interactions with the environment. It has also been demonstrated that the long-range correlations seen in finger tapping (event) and circle drawing (emergent) show very different $1/f^\beta$ properties.³⁹

We sought to answer the following questions: Do long-range correlations affect sensorimotor performance in a general or task-specific manner? Are they reliable across several trials of the same task? In other words, is there a correlation between long-range correlations in circle drawing versus finger tapping? And furthermore, do individuals show the same reliable long-range correlation patterns when performing the same task on different occasions?

To investigate these problems, we looked at the performance of 43 individuals in two timing tasks: unimanual rhythmic tapping and circle drawing.³⁹ In general, we discovered that a participant’s $1/f^\beta$ properties in tapping were not related to the $1/f^\beta$ properties in circle drawing. Within each task, individual differences were extremely reliable.

An examination of Figure 4 reveals that there was very low correlation between the performances on the two timing tasks as revealed by the mean α exponents obtained using detrended fluctuation analysis (DFA) for the series of time intervals. But the analysis of individual subject reliability showed that there was a very high degree of reproducibility within trials. Collectively, our results show that the complex systems being compared represent a consistent and distinctive for each task.

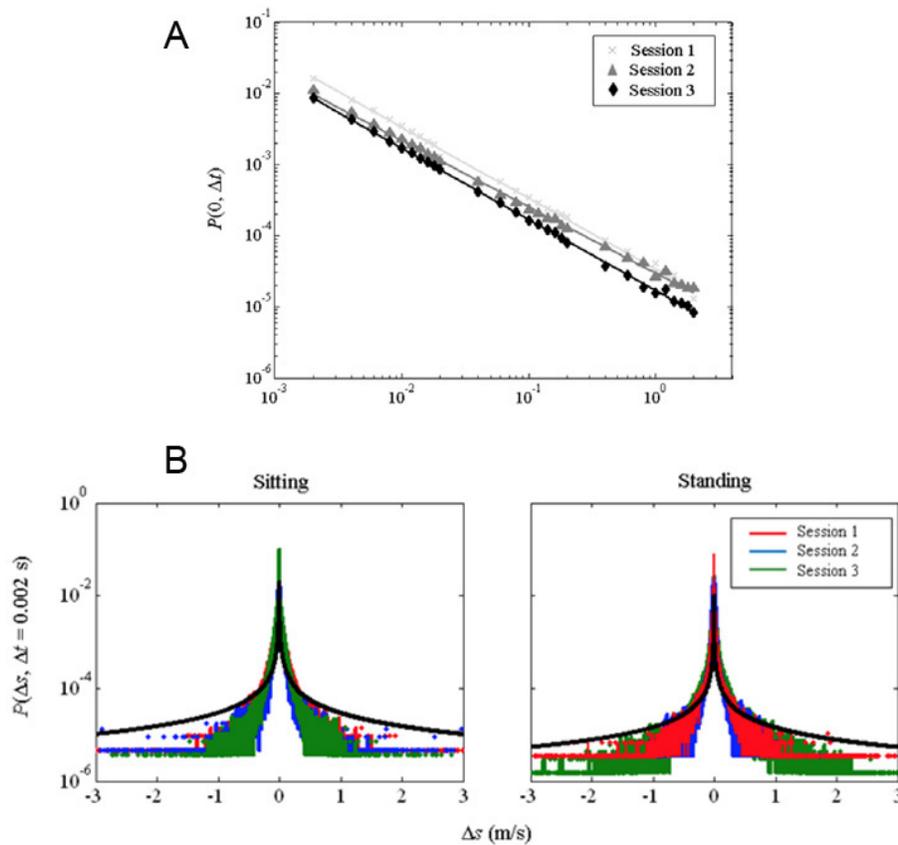


FIGURE 3: The top panel (A) shows a power law distribution for $P(0, \Delta t)$. The bottom panel (B) shows a plot of $P(\Delta s, \Delta t)$ over three sessions in the sitting (left) and standing (right) conditions. The solid black line represents theoretical Levy distribution with (a) $a = 0.95$ and scale parameter $c = 0.03$, and (b) $a = 0.98$ and scale parameter $c = 0.025$. The overlaid theoretical Levy distribution demonstrates both decay exponent a and truncation change with learning in the standing condition. [Reproduced with permission from Cluff et al. (2009), PLoS ONE, Creative Commons license.]

Put simply, individuals show distinctive noise patterns that are reliable and systematic. Once again, the major theme highlighted in this work is that noise that has been measured in the performance of these tasks is an adaptable resource and not a background constraint that needs to be overcome.

III. CONCLUSION AND FUTURE DIRECTIONS

What are some of the important messages that we can glean from this work? The first is a theoretical point about the fluctuations that are seen at all levels in nervous system² as identified in Figure 1.

Noise in biological systems does not need to be “overcome.” Whereas noise can be equated to uncertainty or the presence of randomness in neurobiology, recent evidence suggests that this might not be an accurate characterization. Noise is often correlated. Such correlated noise reveals aspects of self-similarity and scale invariance across levels of the neurobiological system. The presence of correlated noise does not have a predictable relationship with uncertainty. On the contrary, it actually contributes to the state changes that a system might go through. The first set of results from our laboratory highlighted in this review show that the emergence

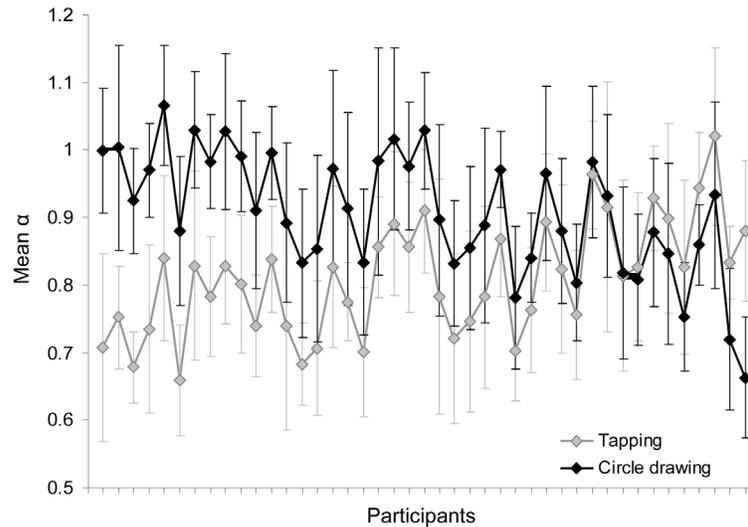


FIGURE 4: Participants ordered along the individual mean differences ($\text{mean } \alpha_{\text{Circle drawing}} - \text{mean } \alpha_{\text{Tapping}}$) after the performance of a detrended fluctuation analysis (DFA). The exponents in circle drawing were higher than those for finger tapping. The participants produced specific levels of serial correlations, as indicated by the matching shapes of the two curves. The crossing of the two curves shows that some participants produced higher α exponents in circle drawing than in finger tapping, while other participants did the opposite. This interaction between the participant and task effects is confirmed by the absence of significant correlation between the α exponents obtained in finger tapping and circle drawing. [Reproduced with permission from Torre et al. (2011) *Psychonomic Bulletin & Review*. ©Springer.]

of specific kinds of correlated noise creates the backdrop for state and phase transitions in behavior. Our research has demonstrated that noise plays a fundamentally different role in a steady state (as studied by Faisal et al.²) than it does surrounding a behavior change or spontaneous phase transition.³³ We have suggested the relationship between local variance (traditional noise) and serial correlation as a potential resource that the neurobiological system could use in remaining stable and flexible.

The second theme we explored was how changes in expertise after skill acquisition can be shown as the nature of changes in a Lévy distribution.^{29,35} The quantification of noise in terms of its distributional properties is useful in determining the nature of corrective processes and learning. The short and long time-scale corrective movements revealed by intermittency have provided insight about the discontinuous nature of the control system that is governing a system in which time

delays make it impossible to rely on feedback control alone.^{37,38}

And finally, we have shown that individual differences in performance have unique signatures that are testable using long-range correlation methodologies.³⁹ What makes one neurobiological system, such as a human, different from another is not just in the structural architecture of the system but also in functional linkages across time scales that emerge in repeated patterns as a behavior unfolds.

Where does that leave the field of complexity in neurobiology? There are several exciting directions of research ahead that we can identify here. An important first step is to scientifically explore the relationship between dynamic functional and effective connectivity patterns that underlie human cognition and the neural substrate on which this activity takes place, while being sensitive to noise in all forms.⁴² Network analysis based on graph theory, especially scale-free graphical models,

will advance our understanding of flexible, stable, and adaptive behaviors that are made possible by a “noisy” brain. Small-world networks, scale-free architectures, and functional connectivity models offer such possibilities.^{42,43}

A interesting path forward for such models and functional brain networks is the treatment of cognitive functions as emergent, metastable patterns of coordination among the levels of brain, behavior, and environment.^{18,22,23} Such models should pay close attention to behavior in steady-state contexts and surrounding critical periods. Some already do.⁴⁴ By examining coordination at these time scales of interaction, we have achieved a meaningful position from which to tackle complexity in all of neurobiology. Several contributions in this volume have successfully taken on this challenge already.

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