

**Soft-Assembly of Sensorimotor Function****Christopher T. Kello**, Cognitive Science Program, University of California Merced**Guy C. Van Orden**, Department of Psychology, University of CincinnatiRUNNING HEAD: Relative coordination, metastability, and pervasive  $1/f$  scaling

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*Abstract: Von Holst (1939/73) proposed relative coordination as a general characteristic of sensorimotor functions like locomotion. Its functionality derives from striking a balance between independence versus interdependence among component activities, e.g., fin or leg oscillations in lipfish and centipede models, respectively. A similar balancing act in the Ising (1925) model was found to produce patterns of electron spin alignment, analogous to the soft-assembly of locomotive patterns. The Ising model analog to relative coordination is metastability, and Kelso (1995) hypothesized that metastability is essential to sensorimotor functions across levels and domains of analysis, from individual neurons to neural systems to anatomical components of all kinds. In the present survey, relative coordination and metastability are hypothesized to underlie the soft-assembly of sensorimotor function, and this hypothesis is shown to predict 1/f scaling as a pervasive property of intrinsic fluctuations. Evidence is reviewed in support of this prediction from studies of human neural activity, as well as response time tasks and speech production tasks.*

KEYWORDS: 1/f noise, long-range correlations, metastability, criticality, relative coordination, soft-assembly, sensorimotor function

Human activities such as reading, speaking, walking, and especially responding in laboratory experiments are typically analyzed in terms of domain-specific mechanisms. A category response “BIRD”, for example, to a laboratory stimulus “sparrow” begins with sensation proceeds to perception, then response selection and finally response execution – a chain of components aligned to accomplish the specific task of categorization. The response time paradigm is quintessential in this regard, in which a stimulus is presented and subjects respond quickly, as soon as the stimulus is perceived and response selected. The time from stimulus presentation to response execution is measured to investigate components of the domain-specific causal chain connecting stimulus to response.

A hierarchy of components is involved in any given sensorimotor function, from individual neurons to the largest anatomical components. Whichever components are investigated, they are assumed to play specific roles in any given sensorimotor chain. For instance, vision components may play the role of letter identification in responses to printed words, and speech components play the role of response execution if the task is to read words aloud. Studying human behaviors as chains of processing components has long been a productive enterprise in terms of describing the demands and constraints imposed by particular tasks.

However, this focus on domain-specific mechanisms leaves open general questions about how sensorimotor components combine and recombine in behavior. How are components coordinated to implement human activities? In particular, what allows component activities to coordinate themselves into a specific function, while at the same time maintaining the potential to re-coordinate into other functions as needed? This deeper question of coordination is not usually addressed in domain-specific theories and is the topic of this article. Empirical motivation to study coordination of sensorimotor functions is demonstrated by laboratory studies of task switching, dual-tasking, and multi-tasking. In these and related paradigms, subjects juggle two or more tasks that may share sensorimotor components. For instance, visual pathways will be shared if the juggled tasks employ visual stimuli, and likewise for motor pathways if tasks employ manual responses.

Our current focus is on how components flexibly reorganize in response to task demands. One answer, implicit in some explanations, is that executive control processes or homunculi must direct the coordination of components (Monsell, 2003). Each particular chain may correspond to a sensorimotor program, for instance, and control processes select among programs and execute them (e.g. Meiran, 2000). The well known problem with this answer is that it merely shifts the burden of explanation onto control processes, and begs the question of the origins of specialized processes (Hollis, Kloos, & Van Orden, in press; Oyama, 2000; Shaw, 2001).

We may also ask about the source of programs to compose the vast range of diverse sensorimotor functions needed over time. The usual answer is that each modular program derives from natural selection, or derives from yet smaller component mechanisms that are products of natural selection (e.g. Barrett & Kurzban, 2006). To illustrate, it is uncontroversial that neuroanatomical pathways between sensory and motor brain regions have been shaped by natural selection, because these pathways are necessary for survival. For instance socializing, foraging, and mating all require both perception and action. If these three specific functions were specific to three separate neuroanatomical pathways, then one could appeal to natural selection as their source.

But this logic immediately runs into the problem that component functions have many-to-many relationships with neuroanatomical pathways. On the one hand, a given function may be implemented in a number of different ways, as evidenced by the remarkable plasticity of biological organisms to re-implement functions when pathways are damaged or otherwise unavailable (Robertson & Murre, 1999; Thulborn, Carpenter, & Just, 1999). On the other hand, any given pathway is involved in many distinct functions if we define function at the organism level of human behavior. Thus the many-to-many relationship makes it difficult to localize functions inside fixed components of neural hardware. It is more intuitive for functions to span neural and bodily components, where each component may play different roles to varying degrees over time. The transience of component roles makes functions appear as changing patterns of neural and behavioral activity.

So to reiterate, what enables sensorimotor patterns to flexibly organize and reorganize into sensorimotor functions? We can begin to answer this question by first recasting natural selection as a kind of coordination itself, in contrast to the watchmaker that creates and assembles component activities (Depew & Weber, 1995; Goodwin, 1994; Kauffman, 1993). Coordination is the fundamental process and functional behaviors are its products, or so we assume in this article. The result is *soft-assembled* functions, i.e., components coordinated and configured by virtue of their properties, interactions, and context (Kloos & Van Orden, in press; Turvey, 1990). On this view, natural selection shapes constraints on interactions among neuroanatomical components such that their coordinations are flexible and adaptive. The word “soft” in soft-assembly denotes the capacity to form temporary organizations, specific to task and context, that may also reorganize to suit changing task demands. The word also serves to contrast with the notion of hard-assembled functions, that is, functions whose particular neuroanatomical components are dedicated to play fixed, specific roles.

In the present article we review and expand upon a theoretical principle that has been proposed to enable soft-assembly (Kello, Anderson, Holden, & Van Orden, in press; Kello, Beltz, Holden, & Van Orden, 2007). The principle is *metastability* and we explain it using formal models of *criticality* (Sornette, 2004). The Ising (1925) model in particular demonstrates formal conditions that give rise to metastable patterns. Metastable patterns have a potential for reorganization that is defining of soft-assembled functions, albeit the Ising model is not a model of sensorimotor function per se. To illustrate the functional potential of metastable patterns, we review models that use them to implement perceptual and cognitive-like processes.

From these models and other related work, we derive a general prediction: *If sensorimotor functions are soft-assembled as metastable patterns, then  $1/f$  scaling should pervade the intrinsic fluctuations of sensorimotor neural and behavioral activity.* We review neurophysiological evidence that corroborates this prediction, and also two recent behavioral studies wherein otherwise paradoxical data support the prediction. We conclude by setting a course for further investigations into the metastability of sensorimotor functions.

### Relative Coordination

In the early 1900s, Erich von Holst identified two opposing principles in animal models of locomotion that together help to explain movement coordination. In this section we review von Holst’s overarching concept of *relative coordination* which serves to illustrate the functionality of metastability. Also in the early 1900s, Ernst Ising formulated a model of

ferromagnetism in which two opposing principles explain spatial patterns of electron spins on a grid. We review the Ising model as well and then draw parallels between von Holst's relative coordination and criticality and metastability, the latter two growing out of Ising's model.

Von Holst's studies of movement coordination focused on bodily components like fins and legs, and their dynamics in locomotion. Coordination of limbs can be described with respect to phase relations among component oscillations. In his studies of limb phase relations in the lipfish and the centipede, von Holst discovered the influence of two opposing principles. On the one hand, each lipfish fin or centipede leg was observed to have its own preferred frequency of oscillation, which von Holst called its *maintenance tendency*. On the other hand, pairs of fins in the lipfish, or the many legs of the centipede, were also observed to be drawn together to oscillate in synchrony, which von Holst called the *magnet effect*.

The most important observation, however, was the joint operation of maintenance tendency and magnet effect. Neither principle by itself accounted for locomotion. For instance, if limb oscillations were driven solely by their maintenance tendency, then phase relations among limbs would yield a flat probability distribution of phases, from in-phase to anti-phase, because components would oscillate independently of each other. If driven solely by the magnet effect, limbs would stay precisely in-phase, resulting in a spiked probability distribution at that phase.

Thus von Holst's critical observation was that locomotion over time is driven neither by the magnet effect nor the maintenance tendency but by the balanced combination of these two principles: Limb oscillations may fall into regularly patterned phase relations to a degree (magnet effect), but limbs also go in and out of phase as each limb is drawn to its preferred frequency (maintenance tendency). Provided that other factors are random and independent, the probability distribution of phase relations will tend to have a mean at in-phase with normally distributed deviations from the mean (see Figure 1).

This balance of maintenance tendency against magnet effect defines relative coordination. A classic illustration is that of a parent and child walking hand in hand. There will be a tendency for strides to be in-phase, but strides also fall out of phase because the longer legs of the taller parent have a lower preferred frequency than the short legs of the child. The result is strides that are in-phase for periods of time, but that also drift into other phase relations depending on frequency ratios and extraneous factors. That is, there are intermittent periods of in-phase strides (Kelso, 1995).

Relative coordination is the hypothesized basis for soft-assembly of locomotion in animal models like the lipfish and centipede. The functionality of relative coordination can be further illustrated in the centipede (see Van Den Berg, 2000). Centipedes crawl by oscillating their legs in traveling waves that move along their length from anterior to posterior. By varying phase relations among legs over time, a spatiotemporal pattern of leg activity is generated that satisfies locomotive needs of the centipede as well as metabolic constraints on energy efficiency.

The centipede crawl does not generalize to other bodily forms, such as four and six-legged creatures, because different organisms require different locomotive patterns to satisfy particular anatomical, physiological, and environmental constraints. The constraints inherent to four and six-legged organisms, for instance, typically result in movement patterns for which adjacent pairs of legs oscillate in an anti-phase relation to each other. These phase relations

are different than the centipede crawl, and such differences across species have sometimes been interpreted to imply different genetically determined motor schema to execute different locomotive functions (see Katz & Harris-Warrick, 1999) – the antithesis of soft-assembled functions.

Nevertheless, von Holst discovered that the different patterns do not require different motor schema; each pattern will emerge in a context of appropriate constraints. To corroborate this idea, Von Holst selectively amputated the legs of centipedes producing four or six-legged creatures, and he observed how they coped with their new bodily constraints. Remarkably, centipedes recovered locomotive function almost immediately and engaged phase relations of leg oscillations appropriate to four or six-legged creatures. They walked in the gaits of quadrupeds or insects.

In the case of the centipede, natural selection has favored a sensorimotor system that flexibly and robustly soft-assembles gaits under a wide range of conditions (Kauffman, 1993). Particular coordinations are determined by the specific constraints in place, such as the number of working legs (for a similar discussion in terms of manual functions, see Schieber & Santello, 2004). The genome may contribute constraints that figure in these coordinations, but it does not contribute explicit motor schemas. The limb coordination of locomotion is generated by intrinsic dynamics and interactions among movement components. Locomotion is a soft-assembled function.

### Criticality and Metastability

Von Holst generalized the idea of relative coordination to include neural oscillators (von Holst, 1996), and we propose to generalize it further by analogy to principles of criticality and metastability developed in statistical physics. This connection is made via the balance between independence (maintenance tendency) versus interdependence (magnet effect) among component activities. Von Holst focused on fin and leg oscillations as component activities, whereas models of criticality and metastability have been applied more broadly to many different kinds of component activities in physical, biological, and social systems (Bak, 1996; Sornette, 2004). The generality of these models stems from the way they are formalized. Here we review two such models and relate them to relative coordination.

First is the famous Ising model, a pillar of statistical physics. The model was originally formulated with respect to ferromagnetism, and its range of impact grew from a generalizable two-dimensional version in which electrons are arranged on a grid (Onsager, 1944). Each electron is represented simply as having either a positive or negative “spin,” and spins are determined by two contrasting factors. Thermal noise, the counterpart to the maintenance tendency, creates a tendency towards disorder in which components act independently of each other. Nearest neighbor interactions, the counterpart to the magnet effect, create a tendency towards coordination and order. Nearest neighbor interactions are formalized by a simple rule stating that spins tend to align with their four nearest neighbors (external forces can also be added to influence spins).

The relative influence of these counterparts is controlled by a temperature parameter. Higher temperatures increase the effects of thermal noise, relative to neighbor interactions. Once temperature is sufficiently high, the probability of observing positive versus negative spins is equal at 0.5, and each electron’s spin is independent of its neighbors’. When temperature is

sufficiently low, the probability of positive spins goes to 0 or 1 as neighborhood interdependence locks in an all-positive or all-negative grid (i.e., a magnet).

Ising model behavior is less interesting at the previous high and low temperatures because the outcomes are so uniformly described: In both cases, the probability of observing a given spin is the same across electrons. The more interesting situation, what made the Ising model famous, is its behavior when temperature nears a *critical point of phase transition* between uniform phases. Near the critical point, the effect of thermal noise (independent spins) is balanced against neighbor interactions (interdependent spins), and this balance allows complex transient patterns of aligned spins to emerge on the grid.

These more complex patterns have a capacity like relative coordination, i.e., the capacity to reorganize in response to changing conditions. In the centipede model, this capacity was demonstrated in the reorganization of gait after loss of limbs. For the Ising model, this capacity is seen in the reorganization of spatial patterns in response to external forces applied to spins. It derives from a property known as *susceptibility* and it is universal to entire classes of Ising-like models (i.e., universality classes; Sornette, 2004). Near-critical temperatures create a special condition whereby just one flip of a spin can propagate and reorganize an entire grid of spins. Susceptibility to perturbation reflects the balance of thermal noise against neighbor interactions, which creates *long-range dependencies* across the entire grid. Long-range dependencies mean that (spin) correlations between pairs of electrons fall off slowly as an inverse power of distance between electrons. This power law fall-off does *not* have an asymptote at zero, which means that each electron has the potential to affect every other electron on the grid.

Long-range dependencies are important because they allow coordinated spatial patterns to emerge across all spatial scales. This kind of scale free behavior creates *fractal* structure (see Figure 2): Smaller clusters of aligned spins are nested within larger clusters, and nest within themselves even smaller clusters, out to the size and resolution limits of the model (and out to infinity in principle). The fractal structure of near-critical patterns provides another way to understand susceptibility, i.e., single flips may realign the smallest clusters, and realignment at the smallest scales percolates up through larger and larger clusters to reorganize the entire grid.

System behavior near critical points is also metastable (Bak, Tang, & Wiesenfeld, 1987; Stoll & Schneider, 1972): Many different patterns of alignment are potential, and the manifestation of a given pattern does not extinguish the potential for other patterns to appear. This is strongly reminiscent of relative coordination in which a given pattern of gait does not extinguish the potential for other gaits to appear. Numerous coordinative patterns of leg oscillations exist as latent potentials in the centipede, for instance, and manifestations of the centipede gait do not extinguish the potentials for quadruped gaits, were only two pairs of working legs to be available. Specifically, metastability balances system flexibility (greater entropy over pattern probability distributions) with the capacity to hold patterns as latent potentials.

The simplicity of the Ising model makes it useful for understanding criticality and metastability. However it is too generic to serve as a model of any particular sensorimotor behavior. We do not know of any Ising model of locomotion, for instance. Nonetheless, Usher et al. (1995) described a model with “Ising properties” of neural center-surround receptive

fields, and the model exhibits metastability near its critical point. The model consists of neuron-like processing units laid out on a grid. Each unit is connected to neighboring units as a function of distance. That is, nearby units receive excitatory connections and more distant units receive inhibitory connections (hence center-surround). Units also receive excitatory inputs from an externally controlled source, and activation dynamics are based on a simple integrate-and-fire equation.

The balance between independence and interdependence can be parameterized by scaling the strength of external inputs with respect to inter-connections among neuronal units. Simulations showed that conditions of sufficiently weak external activation mimic high temperature thermal noise. These conditions preclude stable patterns of activity across the neuronal grid, and yield a disordered (fluid) state. Sufficiently strong external activation created a tendency towards strictly ordered (crystalline) states, expressed as fixed patterns of evenly spaced clusters that reflect the center-surround structure. Near a critical point, however, metastable patterns emerged due to the critical balance between strengths of external inputs and internal connection strengths. Near this critical point, interactions among neuronal units were sufficiently strong to organize patterns, and sufficiently weak to allow re-organization of patterns with changes in external activity.

Usher et al. (1995) examined closely the effects of criticality and transient external activity. One finding was that critical point dynamics were necessary for the model to “remember” previous external inputs, and at the same time respond to new external inputs. Flexible memory seems like an advantageous attribute in all sensorimotor functions, which further motivates consideration of metastability as a general principle of soft-assembled function. This generalization motivated the empirical tests described next.

### Metastability and 1/f Scaling

In order to test the generality of metastability, we need an empirical signature of metastability that is distinctive and measurable across levels of sensorimotor analysis. To illustrate by contrast, consider that Usher et al. (1995) cited optical imaging data (Van Essen & Orbach, 1986) as evidence for fluctuating center-surround patterns consistent with those predicted by their model. Such evidence is useful for testing domain-specific aspects of their model, but not the underlying domain-general principles. We require evidence that is potentially observable in every domain and at every level of sensorimotor function.

Indeed, the fractal structure associated with metastability (e.g. Bell & Southern, 1988; Southern & Achiam, 1993) is not only measurable across domains and levels of analysis, but has been found throughout nature (Mandelbrot, 1982). However, fractals at large cover very broad classes of phenomena and hence are not particularly distinctive of metastability<sup>1</sup>. Fractal patterns of spin clusters, for instance, reflect aspects of the model’s grid geometry, and hence cannot serve as a general empirical signature of metastability. Instead we need to examine *intrinsic fluctuations* in spins as the Ising model unfolds in time (for Ising model dynamics, see Fisher & Huse, 1986).

Intrinsic fluctuations are generally observed when any given series of measurements is taken repeatedly with minimal perturbation or contingencies from extrinsic sources. Ising model intrinsic fluctuations, for instance, can be observed in the summation of spin values (i.e. net magnetization) as a model’s dynamics unfold in time. In the Ising model and other models



of criticality, intrinsic fluctuations exhibit *long-range dependencies* in time (Fisher & Huse, 1986), so called *fractal time*, analogous to fractal spatial patterns. These temporal long-range dependencies more often are called *1/f noise* (see <http://www.nslj-genetics.org/wli/1fnoise>). However, to avoid misleading connotations of “noise”, we use an equivalent term, *1/f scaling*, that highlights scaling properties of fractals.

The term *1/f scaling* denotes a relation between power and frequency when fluctuations in data series are analyzed in the frequency domain, as in a spectral plot (see Figure 3). A time series can be transformed into the frequency domain by Fourier analysis which represents the series as a set of sine waves, each with an associated frequency and amplitude (and power equals amplitude squared). For *1/f* fluctuations, power and frequency are inversely related, and the scaling relation is parameterized by an exponent  $\alpha$  ( $1/f^\alpha$ ) where  $\alpha = 1$  for ideal *1/f* scaling. Fractal structure is seen in an example time series by viewing it at different resolutions or scales of time (see Figure 4). At finer scales, high-frequency, low-amplitude fluctuations are seen to be nested within lower-frequency, higher-amplitude fluctuations. At coarser scales, even lower-frequency, higher-amplitude fluctuations become visible, and in the ideal this nested structure repeats itself out to the lowest and highest frequencies measurable.

*1/f* scaling also reflects a balance that is closely related to the balance of independence versus interdependence. On one side, when  $\alpha = 0$ , sampled values in the time series are independent of one another (i.e., white noise). On the other side, when  $\alpha = 2$ , each sampled value is fully dependent on the previous one, plus a random deviation (i.e., as in Brownian motion). When  $\alpha = 1$  independence is balanced against interdependence.

The association of *1/f* scaling with metastability, that the Ising model dynamics illustrate, provides us with a general testable prediction: If sensorimotor functions are products of a metastable system, then intrinsic fluctuations in sensorimotor activity should exhibit pervasive *1/f* scaling. We derived this prediction using the Ising model, but it stems more generally from all models of criticality and metastability. This includes Usher et al.’s (1995) model of center-surround neural receptive fields, which exhibited *1/f* intrinsic fluctuations in neuronal inter-event intervals, and other models that simulate critical-point dynamics (Bertschinger & Natschlager, 2004; Christensen, Olami, & Bak, 1992; Kwok & Smith, 2005).

The emphasis in this prediction is that *all* measurements of intrinsic fluctuations of sensorimotor processes should exhibit *1/f* scaling, across all levels and domains of analysis—even multiple simultaneous measurements. This pervasiveness comes from the assumption that metastability is an essential property of sensorimotor functions. If so, then individual neurons and individual limbs, for instance, should all express intrinsic fluctuations as *1/f* scaling. Measurements of intrinsic fluctuations should exhibit *1/f* scaling, regardless of whether activities are correlated across components or not. Pervasive *1/f* scaling cannot be isolated in any particular component or set of components.

### Intrinsic Fluctuations of Sensorimotor Systems

A sufficient test for pervasive *1/f* scaling requires that intrinsic fluctuations be measured from multi-level sensorimotor activities – behavioral and neural. In all cases we require measurement series of sufficient length to span three orders of scale magnitude, i.e., at least 1000 measurements. Three orders of magnitude is a practical threshold for taking seriously that one may actually confront *1/f* scaling. Alternatively short-range correlated fluctuations may

mimic the long-range correlations of  $1/f$  scaling, but recently developed model testing methods favor a  $1/f$  scaling conclusion for behavioral intrinsic fluctuations (Kello et al., in press; Thornton & Gilden, 2005).

Using model dynamics as our guide, we require repeated measurements of activity under measurement conditions that are (virtually) identical and that avoid creating contingencies from one measurement to the next (Beltz & Kello, 2006; Gilden, 2001; Van Orden, Holden, & Turvey, 2003). For example, intrinsic fluctuations in neural activity are measured by keeping an organism inactive and taking repeated measurements of “resting state” neural activity, which is ongoing even while organisms are inactive. Resting state neural activity has been investigated in a number of studies, and almost all appropriately conducted studies have observed  $1/f$  scaling (Buzsáki, 2006). The variety of evidence spans cellular to systems levels of analysis; it includes current flow through neuronal ion channels (Banerjee, Verma, Manna, & Ghosh, 2006), rate of neurotransmitter secretion (Lowen, Cash, Poo, & Teich, 1997), interspike intervals between action potentials (Bhattacharya, Edwards, Mamelak, & Schuman, 2005), fluctuations in local field potentials (Leopold, Murayama, & Logothetis, 2003), amplitude levels within EEG and MEG frequency bands (Linkenkaer-Hansen, Nikouline, Palva, & Ilmoniemi, 2001), fluctuations in inter-channel EEG synchronization (Gong, Nikolaev, & van Leeuwen, 2003; Stam & de Bruin, 2004), and voxel activations in functional magnetic resonance imaging (fMRI; Thurner, Windischberger, Moser, Walla, & Barth, 2003; Zarahn, Aguirre, & Desposito, 1997).

Resting state behavioral activity most directly translates into tasks for which movement is minimized, i.e. homeostatic tasks such as standing still. Consistent with the extension of intrinsic fluctuations from neural to behavioral activity, fluctuations in postural sway have been shown to follow a  $1/f$  scaling relation (Duarte & Zatsiorsky, 2001). More generally, intrinsic fluctuations of  $1/f$  scaling are evident generally in repeated measurements of motor behaviors (Riley & Turvey, 2002).

Locomotor tasks are good examples in this regard because they require repeated movements. In the case of walking, for instance, intrinsic fluctuations will appear in measurements of self-paced walking taken at a given point in each stride cycle of leg flex and extension. Hausdorff and his colleagues (Hausdorff, Peng, Ladin, Wei, & Goldberger, 1995; Hausdorff et al., 1996) examined inter-stride intervals, and step and swing durations using detrended fluctuation analysis (Peng et al., 1994). Intrinsic fluctuations in all measurement series exhibited evidence of a  $1/f$  scaling relation.  $1/f$  scaling evidence has also been found in multiple, simultaneous, and distinct measures of kinematics in self-paced walking (Jordan, Challis, & Newell, 2007; Terrier, Turner, & Schutz, 2005). The latter results speak to its predicted pervasiveness.

Another prime example of sensorimotor behavior is eye movements and fixations. Once again the elicitation of intrinsic fluctuations requires repeated measurements under relatively constant conditions. For instance, Shelhamer and Joiner (Shelhamer & Joiner, 2003) instructed participants to fixate back and forth on a regularly alternating visual cue appearing in two constant locations left and right of center. Fluctuations in inter-fixation intervals were found to follow a  $1/f$  scaling relation. Aks, Zelinsky, and Sprout (2002) also found evidence of  $1/f$  scaling in over 10,000 eye movements and fixations in a challenging visual search task (find the upright T in a field of rotated Ts).

Taken together, the studies reviewed thus far provide evidence for  $1/f$  scaling across several levels and domains of sensorimotor function. In this regard, one can also point to cognitive studies that find  $1/f$  scaling across repeated measurements of response time in cognitive tasks (Gilden, 1997, 2001; Kelly, Heathcote, Heath, & Longstaff, 2001; Van Orden et al., 2003). Thus the universality of  $1/f$  scaling to sensorimotor and cognitive systems is becoming increasingly clear. Its pervasiveness, however, does not directly follow from universality because evidence of pervasiveness requires multiple, simultaneous measurements of intrinsic fluctuation. Such evidence has been found in neural (Bhattacharya et al., 2005; Thurner et al., 2003) and locomotor (Jordan et al., 2007; Terrier et al., 2005) activity, but it is not commonly found in cognitive behavioral studies because experimental tasks are usually simple and tightly constrained to focus on one or a very few measured values, usually averaged across trials. We thus require a task with sufficient behavioral degrees of freedom, to promote opportunities to take multiple simultaneous distinct measures.

Pervasiveness is demonstrated when the intrinsic fluctuations of multiple, simultaneous, distinct measures all reveal  $1/f$  scaling. Otherwise it is too easy to intuit that  $1/f$  fluctuations come from one, or a few, domain-specific “hard-assembled”  $1/f$  generators, as has been suggested elsewhere (Pressing & Jolley-Rogers, 1997; Wagenmakers, Farrell, & Ratcliff, 2004). To our knowledge, the first studies to examine this particular issue in cognitive measures looked at two, simultaneous, distinct measures of key press responses – response time itself and the duration of key contact before it was released, i.e. key contact duration (Kello et al., 2007). Four experiments using four different two-alternative forced choice tasks all yielded distinct (uncorrelated)  $1/f$  scaling in the two measures. Furthermore, manipulations of response cue predictability showed that  $1/f$  scaling in response times could be perturbed (“whitened”) without affecting  $1/f$  fluctuations in key-contact durations.

If metastability is the basis for soft-assembling sensorimotor functions, then  $1/f$  scaling should further pervade cognitive behavioral kinematics. It could be argued that two parallel and independent  $1/f$  fluctuation series does not go far enough. A stronger test of pervasiveness could examine dozens or even hundreds of parallel measurement series. Repeated speech provides an apt test bed in this regard. A spoken word requires the coordination of numerous muscle groups in the tongue, lips, jaw, velum, larynx, and lungs. These effectors comprise many degrees of freedom and have the potential to generate many simultaneous, distinct measurement series, each of which could be examined for  $1/f$  scaling.

In an actual example, participants were instructed to speak the word “bucket” repeatedly at a metronome pace of one repetition every 1200 ms (Kello et al., in press). Individual syllables were extracted from acoustic recordings (*bucket* was chosen because its acoustic properties facilitate automatic extraction), and an acoustic spectrum was computed for each syllable. Each spectrum yielded 45 intensity values across the range of frequencies covering audible speech energy (see Figure 5), resulting in a total of 90 measurement series per participant.

Fluctuations in each measurement series were subjected to spectral analysis to test and gauge their  $1/f$  scaling relation. Log power estimates were averaged across all measurement series and all ten speakers for each syllable, and graphed as a function of log frequency (Figure 6). The graphs showed that syllable averages closely followed the  $1/f$  scaling relation. An exponent was also estimated for each individual measurement series (Thornton & Gilden,

2005), and the distribution of exponents was well fit by a normal curve with mean  $\alpha = 1.08$ , which is near ideal  $1/f$  scaling ( $\alpha = 1$ ). The distribution was contained by the lower bound of ideal white noise ( $\alpha = 0$ ) and the upper bound of ideal brown noise ( $\alpha = 2$ ).

Clear evidence for pervasive  $1/f$  scaling in the repetition of a spoken word provides strong support for metastability as a domain-general explanation. To further investigate the pervasiveness of  $1/f$  scaling, Kello et al. (in press) also examined whether multiple, simultaneous, distinct  $1/f$  fluctuation series could be identified in their multivariate data. They conducted a principal components analysis to derive mutually orthogonal sources of variation, resulting in 90 mutually orthogonal series per participant, each series aligned with one of the principal components and ordered from most to least variance accounted for.

Analyses showed that the strongest components of variation also exhibited the most ideal expression of  $1/f$  scaling ( $\alpha$  closest to 1), and that  $\alpha$  fell towards zero gradually as components decreased in priority. Also,  $\alpha$  was clearly in the range of  $1/f$  scaling ( $> 0.5$ ) for the top 30 orthogonal fluctuation series, which on average accounted for 90% of each participant's data. These results agree with pervasive  $1/f$  scaling demonstrated in neurophysiology, and all these findings together are naturally accommodated by the hypothesis of metastability.

### Conclusions and Future Directions

In this article, we reasoned that universality and pervasiveness of  $1/f$  scaling in sensorimotor functions, across levels and domains of sensorimotor systems, is evidence for a general and essential principle of metastability. Our reasoning was based on arguments originally formulated by Turvey (1990) and Kelso (1995) connecting soft-assembly to relative coordination, and relative coordination to metastability. Our contribution was to elaborate and extend their arguments by discussing metastability together with criticality, and criticality with pervasive  $1/f$  scaling. Observed pervasiveness is important because it is not explained by alternative, domain-specific accounts of  $1/f$  fluctuations, except in an absurd reduction to an open-ended, already large collection of separate domain-specific mechanisms, each one generating a distinct  $1/f$  signal (for a review of alternatives, see Wagenmakers et al., 2004; see Kello et al., 2007, for in-depth explanations of why these alternatives are inadequate for pervasive  $1/f$  scaling).

We are motivated to investigate soft-assembled functions because the alternative—hard-wired sensorimotor programs—does not appear viable. A demonstrated model system of soft-assembly is the slime mold *Dictyostelida*, which assembles primitive sensorimotor behavior out of previously independent single-celled amoeba-like individuals. In a context of adequate resources, the amoebae behave as a dispersed collection of individuals, where each individual forages independently of others in its nutrient-rich environment. But in a context of scarce resources, amoebae assemble to form a multi-cellular organism with identifiable body parts for sensory (resource detection) and motor (locomotion) functions. The collective slime mold, thus equipped, may then seek greener pastures.

For decades, biologists searched for a hard-wired program to explain slime mold assembly, something like “pacemaker” cells that might centrally control the coordinated behavior, but no pacemaker was there to be found. Then theory and evidence came to light showing the slime mold to be a phenomenon of soft-assembly (see Johnson, 2001). Neither centralized control nor a priori structural differences distinguish sensory amoebae from motor amoebae; each

single cell can play either role depending on its relation to other cells and its environment at the time of assembly. This now well-understood system illustrates concretely how functional roles may be products of soft-assembly. Soft-assembled functions of locomotion and resource detection are intriguing insofar as they resemble perception and action in more intelligent creatures. Indeed more cognitive-like functions have been observed in two other slime mold models.

Nakagaki (2000) constructed a slime mold “IQ test” for *Physarum polycephalum*, and this single cell, multi-nuclei slime mold passed the test. Nakagaki situated the slime mold in an intellectually challenging context. Resources were hidden in a maze and, remarkably, the slime mold found the most efficient (shortest) path to resources. Wayfinding in a maze is not plausibly hard-wired in the slime mold genome, and no central executive, no nervous system, exists to plan or strategize in finding the shortest path. Wayfinding exists in this sense as a potential for coordinated activity across cells, which seems to have its basis in cytoplasmic streaming, but is only revealed under constraints of resources hidden in a maze.

In a different IQ test, *Physarum polycephalum*, a large yellow slime mold, served as the sensorimotor brain to control a six-legged robot (Tsuda, Zauner, & Gunji, 2006). The natural behavior of the slime mold is to stay away from bright light and seek out dark and moist environments. With the slime mold in control, the robot also avoids light, to stay only in the dark. Light was shined upon a slime mold, grown to fit a six-pointed star, in which each point of the slime mold “star” controlled one leg of the robot. As light caused the slime mold to move, this movement was sensed by a supporting circuit to transform the movement of the slime mold, to the robot, to escape the light.

Model systems like the lipfish, centipede, and now the slime mold provide insights into principles of soft-assembly. One salient principle is how constraints (e.g., environmental, anatomical, metabolic, and so on) limit function and collapse the potentials of individual amoeba to become parts of a way-finding device or the sensorimotor brain of a robot. Accepting our argument,  $1/f$  scaling is evidence that human performances are fundamentally more like the behavior of slime molds than they are hard-coded computer programs (see also Bates & Elman, 2002; Elman, Bates, Johnson, & Karmiloff-Smith, 1996).

The previous conclusion means that all behaviors are conditioned by embodied and situated constraints, and context effects are the norm. Elaborating this point may eventually resolve disputes that arise when context effects complicate or obviate the existence of hard-wired programs. We may also move past logics of subtraction and dissociation that have failed, so far, to isolate functions of general agreement. Thus we may de-populate the crowded hotel of post hoc resident mental faculties, each one restricted to one kind of behavior. One may replace questions about hard-wired programs with questions about constraints, potentials, and coordination of human performance.

With new questions come new methods for testing new theories. We can only speculate on how progress may unfold, but early on, we see more work being necessary to define the conditions under which  $1/f$  scaling is observed, and when and how results deviate from  $1/f$  scaling. Results from initial investigations are consistent thus far with our empirical definition of intrinsic fluctuation, but the definition needs further testing, particularly its breadth across sensorimotor systems and levels of analysis. Results thus far also suggest that  $1/f$  fluctuations *must* be defined with reference to their measurement conditions (Van Orden, Kello, & Holden,

in press). The kind of reference frame suggested is analogous to how phenomena came to be framed within quantum mechanics, in which probabilistic information about particles is made definite only in the context of measurement (Bell, 1987; Herbert, 1987). This analogy may serve to guide further hypotheses and investigations.

In terms of theory, one important step will be to develop models that use metastability to soft-assemble functions in specific sensorimotor domains, and thereby account for empirical benchmarks of those functions. Usher et al.'s (1995) model of center-surround receptive fields is potentially one such model, but it did not explicitly make use of the computational advantages conferred by metastability. By contrast, Van Leeuwen, Steyvers, and Nooter (1997) used metastability to model perceptual reorganizations that occur when multiple percepts of a given stimulus are possible (e.g., the Necker cube and the Schröder stairs).

Another model that leverages the power of metastability, albeit not in the domain of sensorimotor function, was reported by Kwok and Smith (2005). They built a self-organizing neural network to solve combinatorial optimization problems like the famous traveling salesman problem. A parameter governed the order/disorder of component activities, and model performance was optimal when this parameter was set at the critical point between ordered and disordered phases. The metastable patterns that then emerged enabled the model to more successfully discover globally optimal solutions. Metastability also produced (presumably pervasive)  $1/f$  fluctuations in the model's component activities. Search is a fundamental sensorimotor function, hence this model may prove useful to inspire new simulations of sensorimotor phenomena.

Another fundamental and essential sensorimotor function is categorization. Bertschinger and Natschläger (2004) reported neural network models that, while not sensorimotor per se, demonstrate the power of metastability for purposes of classification (see also Langton, 1990; Packard, 1988). Their networks consisted of randomly connected thresholding neurons (chosen for their biological plausibility), and criticality was assessed as a balance of convergence (order) and divergence (chaos) in network dynamics. The metastable regime during training of models maximized the number and complexity of learned classes. As with Kwok and Smith's (2005) study, the work of Bertschinger and Natschläger may inspire additional simulations using soft-assembly of sensorimotor functions.

In closing, one caveat is that human sensorimotor function has a range and depth of complexity that will not likely be captured by any computational or biological model, not even the slime mold. Human capabilities are far more complex and differentiated, for instance, compared to idealized neurons or single-celled amoebae, or their combinations in models. Human behavior entails indefinitely numerous potentials via complex combinations of constraints within which sensorimotor functions may be soft-assembled. Nonetheless, intrinsic fluctuations so far reveal the dynamics of metastability. This evidence supports a reasonable working hypothesis and simplifying principle with which to go forward. The kind of scale-free dynamics that appear near critical points of complex systems also appear to support the soft-assembly of sensorimotor functions.

## Endnotes

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<sup>1</sup> Researchers debate whether the apparent universality of fractal structure is evidence for universal principles of some kind. We are intrigued by the argument for universality in the larger sphere, but this issue is separate from whether *particular* fractal structures constitute evidence for a given general principle, i.e. metastability in our case.

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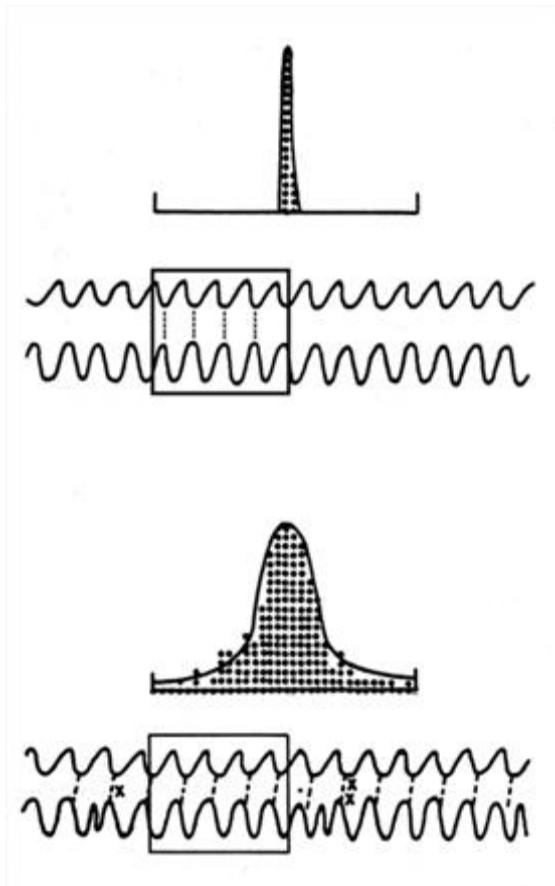


Figure 1. Recordings of limb oscillations taken by von Holst under two different conditions. The top shows dominance of the magnet effect and the bottom shows relative coordination in the balance of magnet effect and maintenance tendency. The waveforms show two limb positions along one axis over time, and the histogram shows the distribution of observed phase relations, centered at in-phase. The intermittency of relative coordination results in greater dispersion, whereas dominance of the maintenance tendency would show even greater dispersion (i.e. nearing a flat distribution across phase relations; not shown).

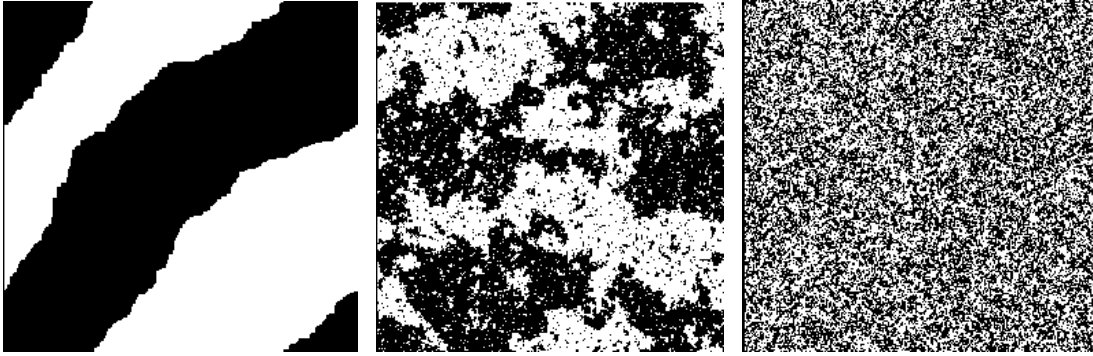


Figure 2. Example plots of site values (positive or negative spins) for a two-dimensional Ising model at low (left), critical (middle), and high (right) temperature values. Low temperature causes spins to align, in the limit becoming all positive or negative, whereas high temperature causes spins to randomize. At the critical temperature, clusters of alignment can be seen at multiple scales of analysis (i.e., as if one zoomed in or out on the grid).

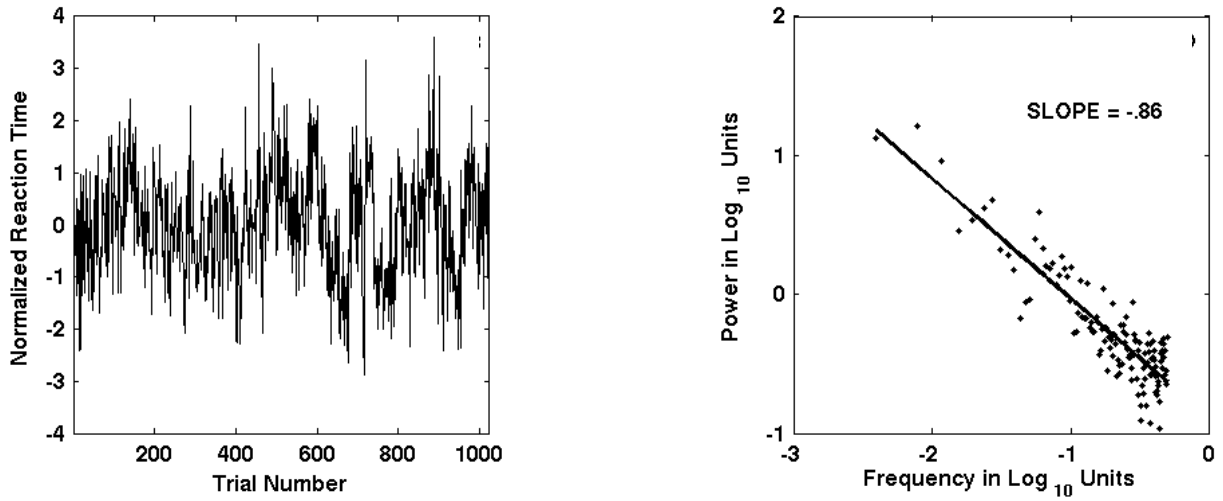


Figure 3. An example of  $1/f$  fluctuations in one participant's series of reaction times (Kello et al., 2007), shown as a time series on the left, and its corresponding spectrum on the right. The spectrum is plotted in log-log coordinates to express the  $1/f$  relation as linear with a slope near  $-1$ .

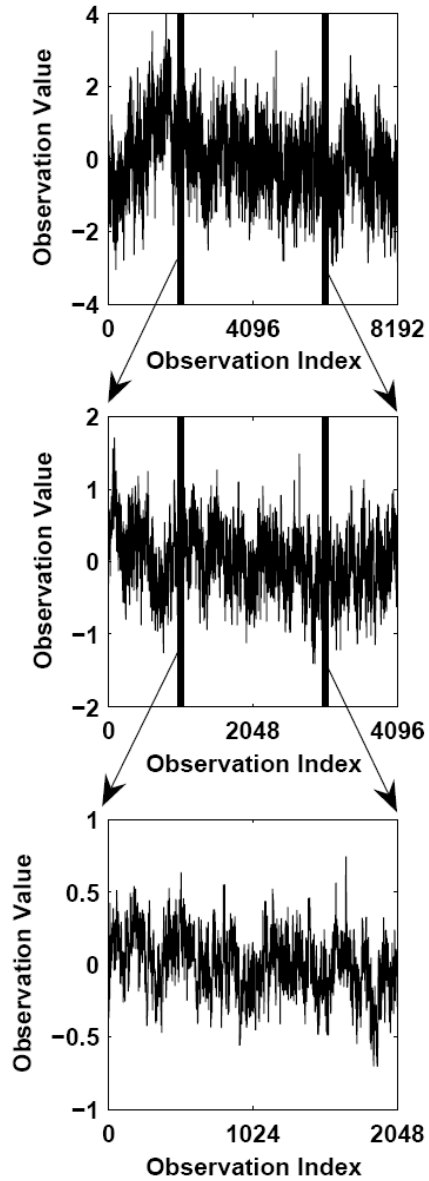
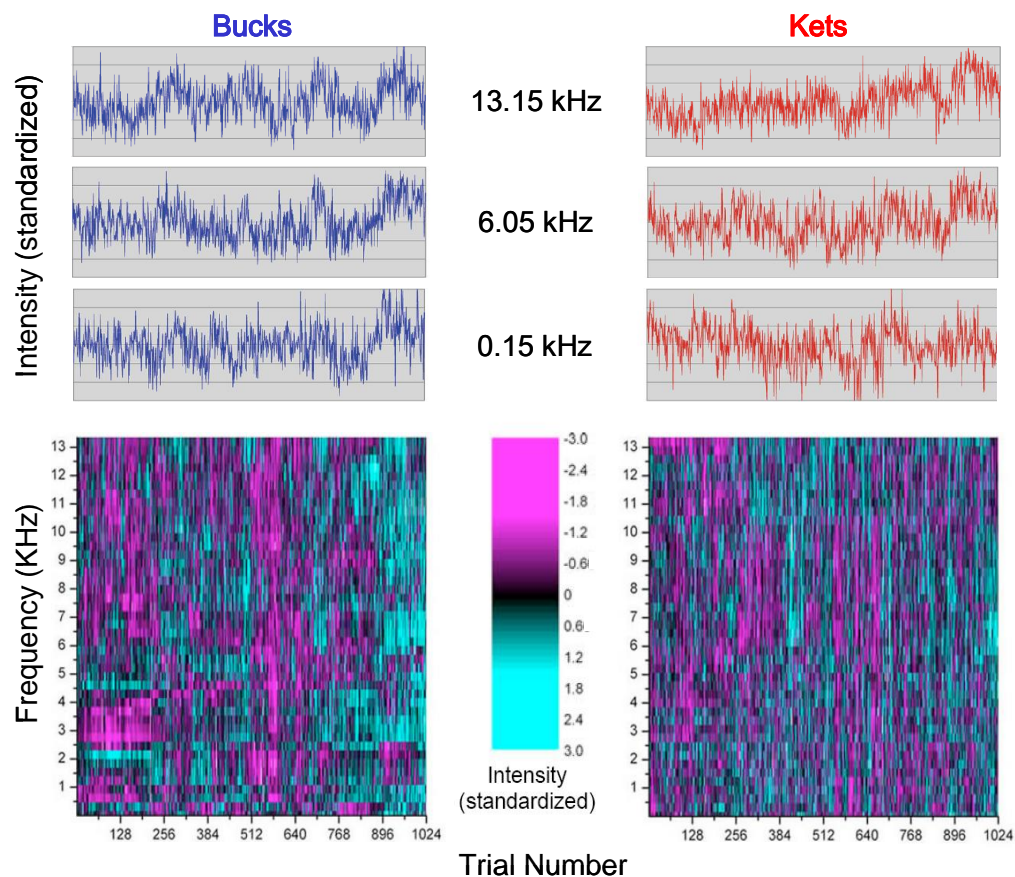
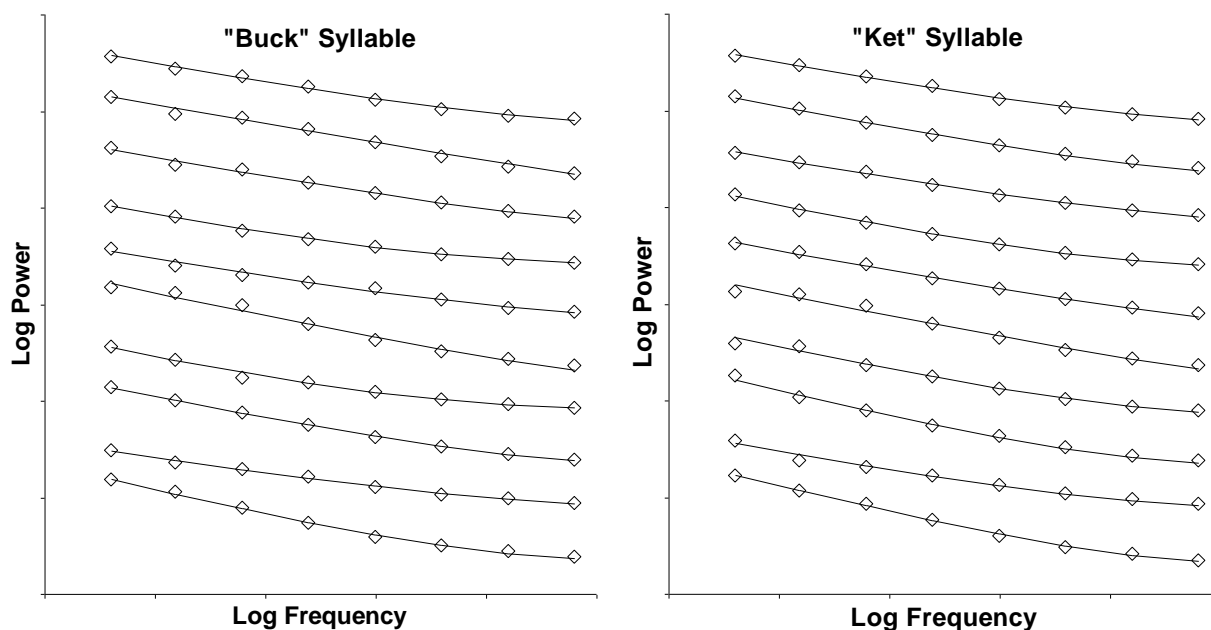


Figure 4. An example series of  $1/f$  fluctuations, plotted at three different time scales to show its self-similar structure (taken from Holden, 2005).



**Figure 5.** Sample series of intensity measurements for one participant taken from Kello et al. (in press). At the top are plotted three example fluctuation series of intensity estimates at three different frequencies for each syllable “buck” and “ket”. To visualize this participant’s full pattern of fluctuations, all 45 intensity series for each syllable are plotted as two spectrograms. Intensity is coded using a magenta-black-cyan color scale, and the trial series is on the x-axis. The spectrograms show that intensity fluctuations were temporally non-random and yet non-identical across frequencies.





**Figure 6.** Average composite spectra are plotted for each syllable and each of the ten participants reported by Kello et al. (in press). The 45 composite spectra for each syllable and each participant were averaged together, and each composite per syllable (“buck” left and “ket” right) and per participant (10 participants, top to bottom) is plotted in log-log coordinates (open diamonds). Participants’ composite spectra are separated in each graph by log units for the sake of visibility. Thorton and Gildden’s (2005) “fractional Brownian motion plus white noise” model was fit to each plotted composite, and the resulting model spectra are shown by the solid lines.