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Connectivity in the human brain dissociates entropy and complexity of auditory inputs☆

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ABSTRACT

Complex systems are described according to two central dimensions: (a) the randomness of their output, quantified via entropy; and (b) their complexity, which reflects the organization of a system's generators. Whereas some approaches hold that complexity can be reduced to uncertainty or entropy, an axiom of complexity science is that signals with very high or very low entropy are generated by relatively non-complex systems, while complex systems typically generate outputs with entropy peaking between these two extremes. In understanding their environment, individuals would benefit from coding for both input entropy and complexity; entropy indexes uncertainty and can inform probabilistic coding strategies, whereas complexity reflects a concise and abstract representation of the underlying environmental configuration, which can serve independent purposes, e.g., as a template for generalization and rapid comparisons between environments. Using functional neuroimaging, we demonstrate that, in response to passively processed auditory inputs, functional integration patterns in the human brain track both the entropy and complexity of the auditory signal. Connectivity between several brain regions scaled monotonically with input entropy, suggesting sensitivity to uncertainty, whereas connectivity between other regions tracked entropy in a convex manner consistent with sensitivity to input complexity. These findings suggest that the human brain simultaneously tracks the uncertainty of sensory data and effectively models their environmental generators.

Introduction

Theoretical and experimental work in the fields of psychology and complexity science has arrived at two separate approaches for describing how stimuli may be encoded and what constitutes a complex stimulus (see Shiner et al., 1999). The first aims at explaining to what extent a specific stimulus can be considered “simple” from the perspective of a machine whose goal is to veridically encode and reproduce that stimulus (e.g., Chater and Vitanyi, 2003). For example, the stimulus *ABCDABCD* is quite simple because it can be represented as “repeats *ABCD* twice,” whereas *ACDDBADC* is substantially more complex because it requires more memory to encode. Within this framework, simple stimuli are therefore those that contain noticeable patterns; they permit compressed representation, are easy to manipulate and provide a basis for predicting future states. Importantly, from this perspective, “complexity” scales monotonically with stimulus disorder (entropy), as more disordered inputs are less compressible—that is, increasingly random stimuli require more memory in order to be veridically reproduced.

On the other hand, the second, more recent view (e.g., Crutchfield, 2012) holds that simplicity/complexity depends on how demanding it is to model the underlying system that generated a particular stimulus or signal via the interactions of its states. From this perspective, there is a convex, inverse U-shaped relation between disorder and complexity. This is because highly ordered and highly disordered signals are typically generated by succinct, easily describable systems, whereas more sophisticated, or complex, systems generally convey intermediate levels of entropy.[1] Note that in this latter approach, complexity does not capture how difficult it is to veridically encode or reproduce any specific stimulus or signal, but rather how computationally demanding it is to model the system or source generating that signal. As can be appreciated, the two views described above are independent, and graphs depicting

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[1] For instance, *ABCDABCD* can be thought of as generated by a system (e.g., a transition matrix) that transitions between four states deterministically (a simple explanation), while a random stimulus can be characterized by a system where all state transitions are equally likely (a similarly simple explanation).

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monotonic vs. convex complexity–entropy relations are the subject of ongoing theoretical discussion (e.g., Feldman et al., 2008).

There has been substantial theoretical and behavioral support, as well as some validation from neuroimaging studies, for the importance of entropy in sensory and cognitive processing, as detailed below. However, there is as yet little evidence that the human brain codes for environmental inputs in a way consistent with the second view arguing for a convex relation. The current study was motivated by the hypothesis that, from a cognitive perspective, these two properties are complementary. In the following, we argue that the human brain tracks both disorder (the degrees of freedom in sensory data) and complexity (quantified, e.g., by the degrees of freedom or minimum message length specifying a model of those data; Spiegelhalter et al., 2002; Wallace, 2005). This sort of dual encoding model suggests that neural sensitivity to uncertainty may vary both linearly and convexly in response to stimuli of increasing entropy. We then present a functional MRI study addressing this hypothesis.

Sensitivity to entropy is crucial for compression (Barlow, 1961; Borst and Theunissen, 1999; Brady et al., 2009; Buiatti et al., 2009; Olshausen and Field, 1996), prediction (Kiebel et al., 2008) and guiding adaptive behavior (Ashby, 1947; Friston, 2010). Prior neuroimaging studies have documented neural systems whose activity monotonically tracks the degree of uncertainty in sensory inputs, particularly in lateral temporal cortex (Bischoff-Grethe et al., 2000; Tobia et al., 2012), the anterior cingulate (Harrison et al., 2006, 2011), and the hippocampus (Strange et al., 2005), even in the context of passive listening (Tobia et al., 2012; Tremblay et al., 2012) or passive viewing (Nastase et al., 2014). Behavioral work has shown that humans track parameters related to entropy, such as token frequency (Shannon entropy; e.g., Berlyne, 1957; Vitz, 1966, 1964), transition constraints (Markov entropy; e.g., Falk and Konold, 1997; Saffran et al., 1996) and chaotic patterns underlying nonlinear systems (e.g., Smithson, 1997). Chater (1996) and Chater and Vitanyi (2003) adopt a monotonic entropy–complexity relation, suggesting that this sort of pattern sensitivity is grounded in a basic cognitive principle: people search for the simplest (i.e., sparsest, most compressed) representation of a given input. This approach operationalizes sparseness or compressibility of a stimulus in terms of Kolmogorov complexity (Kolmogorov, 1965), an information theoretic construct reflecting the length of the shortest computer program that can encode and reproduce the stimulus (e.g., Chater and Vitanyi, 2003). Falk and Konold (1997) provide convincing behavioral support for this perspective in showing that series that are subjectively perceived as more disordered take longer to memorize and are more difficult to copy. Antrobus (1968) furthermore demonstrated that auditory series of greater entropy are associated with fewer task-unrelated thoughts.

While the above studies provide substantial evidence that the brain is sensitive to input entropy, we hypothesized more specifically that certain brain systems would track entropy in a convex manner, indicating sensitivity to complexity. Note that entropy captures only a partial feature of a temporally unfolding environment, namely the uncertainty in the signal generated by a system, rather than specifying the system itself. Researchers in the field of complexity science have quantified "complexity" in terms of the sophistication of a system's underlying structural configuration, whereas entropy captures the randomness or uncertainty associated with a system's output (e.g., Crutchfield, 2012). This formulation of complexity has roots in early work by Huberman and Hogg (1986), which framed complexity in terms of the diversity of interactions among elements of a system across all levels of a system's structural hierarchy. More recent treatments of complexity have followed a similar trajectory: Bialek et al. (2001) emphasized the generalizability of the predictive information captured by models. Crutchfield's structural complexity (Crutchfield, 2012; Feldman et al., 2008) reflects the model sophistication required to specify a system's underlying configuration. Bayesian model selection accounts for complexity in terms of model evidence or marginal likelihood (see Spiegelhalter et al., 2002). The evidence for a generative model relies on a tradeoff between fit and complexity, where complexity effectively measures the degrees of freedom, in terms of model parameters, needed to provide an accurate explanation of the data. In this sense, entropy represents the degrees of freedom in the data, while complexity captures the degrees of freedom used by the model to explain those data. This resonates with current neurocomputational theories of free energy minimization, where approximate Bayesian inference (e.g., via predictive coding) serves to maximize model accuracy and minimize complexity (Clark, 2012; Friston, 2010). These theories are consistent with the hypothesis that the brain encodes both accuracy and complexity.

Independent of the formal details, these latter approaches to complexity converge on a central principle: systems generating either highly structured or random outputs can often be specified in a relatively concise way — that is, in terms of a model with fewer parameters or succinct schema — while systems characterized by more intricate underlying structural interactions tend toward producing outputs of intermediate entropy and require more sophisticated models. Consequently, there is a convex relationship between entropy and complexity such that complexity is minimal in systems generating outputs with extremely low or high entropy, but is maximal somewhere between these extremes (Gell-Mann, 1995; Huberman and Hogg, 1986; Lopez-Ruiz et al., 1995; Shiner et al., 1999).

The above discussion does not constitute theoretical hairsplitting, as it offers a more detailed account of how the human brain may process sensory inputs of varying disorder. For example, neural sensitivity to varying complexity (a curvilinear response to entropy) may reflect the brain's maintenance of a generative model useful for predicting incoming sensory stimuli by inferring their underlying causes (e.g., Dayan et al., 1995; Friston, 2010). This abstract model of the environment's structural configuration provides a succinct template useful for generalization and for detecting changes between environmental states.[2] Interestingly, behavioral work has shown that stimuli with intermediate levels of randomness are often considered attention-grabbing, or judged as more interesting, aesthetically appealing or otherwise "complicated" (Berlyne, 1971; Loewenstein, 1994; Vitz, 1966). Abdallah and Plumbley (2009) formally demonstrated that series in which each discrete stimulus reduces a relatively large amount of prior uncertainty are characterized by intermediate levels of disorder; this provides a computational explanation for why such stimuli are perceived as highly engaging.

Given this motivation, we hypothesized that the degree of functional integration within specific networks of the human brain would vary according to both the entropy of an ongoing sensory input as well as the complexity of the system generating that input. To test this hypothesis, we used functional MRI to model the whole-brain connectivity networks of several seed regions while participants passively listened to four 2.5 min auditory series. Each series was characterized by a different level of entropy as determined by the transition constraints between tones. We then used planned contrasts to probe for specific entropy-dependent changes in the regression coefficients of the seed time series.

[2] To illustrate, a model that represents a system as "transitioning between four states deterministically" is consistent with 24 possible instantiations of actual low-entropy outputs (e.g., *ABCDABCD*… or *DBCADBCA*…). Conversely, a random source that generates a continuous series of four tokens can be represented as, "all state transitions are equally likely." These concise descriptions are insufficient for lossless compression or veridically reproducing any specific stimulus generated by a system, but are indeed sufficient for detecting a change from an ordered to a random environment. Most importantly, although the systems generating these series vary greatly in the expected conditional entropy of their output streams (2 bits in the random case, 0 in the deterministic case), both share concise descriptions when specifying state transitions. In contrast, an output such as *ABCDAABCDABCD*… has a conditional entropy somewhere between the random and deterministic cases above, but the system generating this series itself is more challenging to specify, e.g., "generates ABCD consecutively with the exception that A may repeat itself," and therefore can be considered more complex than the random or deterministic case.