# NETWORK NEURO SCIENCE

#### an open access 🔓 journal



Citation: Kardan, O., Stier, A. J., Layden, E. A., Choe, K. W., Lyu, M., Zhang, X., Beilock, S. L., Rosenberg, M. D., & Berman, M. G. (2023). Improvements in task performance after practice are associated with scalefree dynamics of brain activity. *Network Neuroscience*, 7(3), 1129–1152. https:// doi.org/10.1162/netm\_a\_00319

DOI: https://doi.org/10.1162/netn\_a\_00319

Supporting Information: https://doi.org/10.1162/netn\_a\_00319

Received: 13 July 2022 Accepted: 11 April 2023

Competing Interests: The authors have declared that no competing interests exist.

Corresponding Authors: Omid Kardan omidk@med.umich.edu Marc G. Berman bermanm@uchicago.edu

Handling Editor: Olaf Sporns

Copyright: © 2023 Massachusetts Institute of Technology Published under a Creative Commons Attribution 4.0 International (CC BY 4.0) license

The MIT Press

# RESEARCH

# Improvements in task performance after practice are associated with scale-free dynamics of brain activity

Omid Kardan<sup>1,2</sup><sup>(1)</sup>, Andrew J. Stier<sup>1</sup><sup>(1)</sup>, Elliot A. Layden<sup>1</sup>, Kyoung Whan Choe<sup>1</sup>, Muxuan Lyu<sup>1,3</sup>, Xihan Zhang<sup>1</sup>, Sian L. Beilock<sup>1,4</sup>, Monica D. Rosenberg<sup>1</sup><sup>(1)</sup>, and Marc G. Berman<sup>1</sup><sup>(1)</sup>

<sup>1</sup>Department of Psychology, University of Chicago, Chicago, IL, USA <sup>2</sup>Department of Psychiatry, University of Michigan, Ann Arbor, MI, USA <sup>3</sup>Department of Management and Marketing, The Hong Kong Polytechnic University, Hong Kong <sup>4</sup>Barnard College, Columbia University, New York, NY, USA

Keywords: Scale-free activity, Learning and performance, Practice effects, Working memory tasks

# ABSTRACT

Although practicing a task generally benefits later performance on that same task, there are individual differences in practice effects. One avenue to model such differences comes from research showing that brain networks extract functional advantages from operating in the vicinity of criticality, a state in which brain network activity is more scale-free. We hypothesized that higher scale-free signal from fMRI data, measured with the Hurst exponent (*H*), indicates closer proximity to critical states. We tested whether individuals with higher *H* during repeated task performance would show greater practice effects. In Study 1, participants performed a dual-n-back task (DNB) twice during MRI (n = 56). In Study 2, we used two runs of n-back task (NBK) data from the Human Connectome Project sample (n = 599). In Study 3, participants performed a word completion task (CAST) across six runs (n = 44). In all three studies, multivariate analysis was used to test whether higher *H* was related to greater practice-related performance improvement. Supporting our hypothesis, we found patterns of higher *H* that reliably correlated with greater performance improvement across participants in all three studies. However, the predictive brain regions were distinct, suggesting that the specific spatial  $H\uparrow$  patterns are not task-general.

# **AUTHOR SUMMARY**

Individuals vary in the degree to which they improve on a task upon repeating it, referred to as practice effects. Research has shown a relationship between scale-free brain activity and advantageous functional properties for the brain networks. Therefore, we asked if practice effects are related to these scale-free brain dynamics. We hypothesized that individuals with more scale-free fMRI activity, measured with Hurst exponent (*H*), when repeating tasks would show larger practice effects. Across three datasets including different tasks and individuals, we found that higher fMRI *H* was associated with greater task performance improvement. We conclude that exhibiting more efficient information processing when performing a cognitive task may be indexed by higher fMRI scale-free activity and predict further improvement in task performance.

Practice effects:

Any gained performance improvement in a task upon repeating it.

#### Working memory:

The cognitive system that allows for the process of temporarily holding and manipulating information.

#### Executive function:

Set of cognitive processes that allows for directing thought and action toward obtaining the goals of the task at hand.

#### Neural process model:

A model that attempts to elucidate the principles that underlie a certain sensory/perceptual/cognitive process based on information processing and neural computations in the brain.

#### Criticality:

State of complex systems poised at the brink of a phase transition between order and randomness.

### INTRODUCTION

Improvements in cognitive performance due to repeated practice vary considerably across individuals, even within the same task (Calamia et al., 2012). When situational factors and age are controlled, the variability observed in these so called 'practice effects' (see McCaffrey et al., 2013) across healthy individuals is traditionally attributed to differences in intellectual ability, where individuals with higher fluid intelligence benefit more from practice (Rapport et al., 1997). The magnitude of practice effects in multiple tests of working memory, attention, and executive function has been shown to provide rich and unique information about the respondent, and can be used for diagnosis of clinical conditions as well as responsiveness to clinical interventions (Duff et al., 2012). Given the diagnostic and prognostic values of practice effects, it is important to pursue neural process models for explaining differences in cognitive performance improvements from practice.

As there is increasing evidence for the theory that the brain displays critical or near-critical dynamics (Beggs & Timme, 2012), in the current study, we characterized the brain as a network that imparts functional advantages when operating close to or at criticality (see Box 1). We propose that brain network criticality provides a theoretical framework for investigating changes in cognitive performance after practice. Specifically, performing most complex tasks that engage working memory and focused attention depend on active information storage and transfer in neuronal ensembles (Awh & Jonides, 2001; Ikkai & Curtis, 2011). Brain states near criticality would confer computational advantages (i.e., superior information transfer and storage) and such advantages could be measured in neural dynamics that we hypothesized would be tied to differences in learning and practice effects.

# Box 1.

Critical state in a dynamic network. Consider a physical system whose large-scale behavior is not merely the sum of its smaller components (i.e., it is a network with interactions between nodes). Such systems can be in different states based on whether the network configuration is poised at minimum stability or not. As a toy example, the network in Figure 1 (left panel) consists of nodes with active or inactive states, where network dynamics are configured such that an active node becomes inactive at the rate of  $\lambda$  (i.e., decay rate), and activity in a node spreads to a random neighboring inactive node at the rate of  $\gamma$  (i.e., propagation rate). In such a network the time evolution of small-scale local activity can be spread chaotically if  $\lambda < \gamma$  or be absorbed before resulting in global activity patterns if  $\lambda > \gamma$ . At the border between these two regimes  $(\lambda = \gamma)$ , the observed global patterns of activity tend to become self-similar over different temporal and/or spatial scales, that is, they are scale-invariant as they follow the power law distribution where power is directly proportional to frequency (Frette et al., 1996; Muñoz, 2018). In other words, this 'critical' state ( $\lambda = \gamma$ ) separates the subcritical phase  $(\lambda > \gamma)$ , where transient activity decays to a zero-activity steady state, from the supercritical phase  $(\lambda < \gamma)$ , where transient activity turns into sustained global activity (see Figure 1, right panel, for examples of activity spread under each of these states). Therefore, the minimal stability of the network at a critical state enables maximum susceptibility to perturbation by environmental inputs while avoiding sustained global activity that prevents sensitivity to other transient activity (Chialvo, 2004; Fraiman et al., 2009; Frette et al., 1996). One can conceive of brain networks similarly: small-scale neuronal ensembles with short- and long-term interactions (phase-coupled electro-chemical activity) give rise to the emergent large-scale activity linked to cognitive functions (Chialvo, 2010; Cocchi et al., 2017; Fagerholm et al., 2015; Gisiger, 2001; He, 2014; Shew & Plenz, 2013; Werner, 2010). There is evidence of selforganized criticality in the human brain's intrinsic activity (de Arcangelis et al., 2006; Kitzbichler et al., 2009; Suckling et al., 2008), permitting dynamic reorganization into alternative states (i.e., further from criticality) depending on behavioral and cognitive demands (Arviv et al., 2015; Fagerholm et al., 2015; Gollo, 2017; Hahn et al., 2017; Yu et al., 2017).



**Figure 1.** Left: Schematic of the dynamics of deactivation ( $\lambda$ ) of an active node or propagation of activity ( $\gamma$ ) to a neighboring node in a simple network exhibiting nonequilibrium phase transition. Right: Simulating propagation and decay in a one-dimensional lattice of nodes shows how different relationships between activation rate ( $\gamma$ ) and deactivation rate ( $\lambda$ ) results in the network to be in (A) subcritical ( $\lambda > \gamma$ ), (B) critical ( $\lambda \approx \gamma$ ), or (C) supercritical ( $\lambda < \gamma$ ) states.

Large-scale brain network:

Collections of widespread brain regions that are functionally connected as shown by coordinated activity.

#### Scale-free:

When brain activity does not contain a predominant rhythmic temporal scale but has a 1/f-like power spectrum, it is called 'scale-free'.

#### Autocorrelation:

The similarity between a signal and a delayed copy of it as a function of different lags.

Simulated neural networks: Study of simulations on artificial neural networks to model computing in biological neural networks.

A common way to measure the criticality of large-scale brain networks is via estimation of timescale invariance (e.g., the 1/f component of power spectral density function) in brain activity. Specifically, scale-free brain activity has been successfully measured using the Hurst exponent (H) for both electrophysiological brain activity (e.g., EEG, MEG, ECoG) and blood oxygen level-dependent (BOLD) fMRI signals, where higher H indicates more scale-free dynamics. There is some evidence showing that operating near criticality may facilitate learning and plasticity (de Arcangelis & Herrmann, 2010). Higher H characterizes more long-range temporal correlations (LRTCs) corresponding to slowly attenuating autocorrelations in the signal, which coexist with features of a critical state (Bak et al., 1987; Tian et al., 2022). Both criticality and LRTCs have been used to describe brain network dynamics and states (Marinazzo et al., 2014; Meisel et al., 2017b; O'Byrne, & Jerbi, 2022; Vohryzek et al., 2022; Zimmern, 2020). Importantly, operating close to or at a critical state in simulated neural networks has been shown to provide multiple advantageous functional properties for the network. These include improved information storage and transfer (Boedecker et al., 2012; Shriki et al., 2013; Shriki & Yellin, 2016; Tanaka et al., 2008), as well as increased dynamic range (Gautam et al., 2015; Kinouchi & Copelli, 2006) in the network. Other studies have found that LRTCs in cortical activity support the integration of information in brain networks (see Meisel et al., 2017a), especially in tasks engaging working memory that require processing of information over longer periods of time (Chaudhuri et al., 2015; Kiebel et al., 2008; Kringelbach et al., 2015).

Lower *H* in brain activity has been reported for populations with substance use (Ide et al., 2016), attention deficit (Sokunbi, 2018), depression (Wei et al., 2013), general psychopathology (Stier et al., 2023), and mild cognitive impairment (Long et al., 2018) disorders, as well as following sports-related concussions compared to healthy controls (Churchill et al., 2020). Lowered *H* has been found to be correlated with distress and aging (Churchill et al., 2016; Goldberger et al., 2002), and following sleep deprivation (Meisel et al., 2017a). Furthermore, scale-free activity in electrophysiological and fMRI signals has been shown to be suppressed (i.e., decreased *H*) during the exertion of cognitive effort compared to more restful states (Churchill et al., 2016; He, 2014; Kardan et al., 2020; Zhuang et al., 2022). For example, Fagerholm et al. (2015) used combined EEG and fMRI to find that the resting state is associated with near-critical dynamics while a focused cognitive task induces subcritical dynamics.

Additionally, Kardan et al. (2020) found that when individuals were performing a task with trials of low, medium, or high working memory demands, global suppression of *H* in EEG brain activity tracked the task loads, indicating that lowered *H* represents a departure from the state of rest toward an 'effortful' state (i.e., potentially further away from criticality). Notably, the degree of *H* suppression monotonically tracked task demands within individuals better than specific EEG oscillatory components such as alpha power. Furthermore, differences in cognitive performance of healthy individuals has been found to be associated with the *H* component in both fMRI (Stier et al., 2023; Suckling et al., 2008), fNIRS (Zhuang et al., 2022), and EEG (Ouyang et al., 2020), such that higher *H* reflected better working memory performance and faster processing speed, respectively. None of these studies, however, have investigated the relationship of *H* with *changes* in task performance due to learning from practice.

Taking these neural network simulation and human participant studies together, we hypothesized that when an exogenous task demand suppresses slow-decaying autocorrelations or *H*, the ability to process other exogenous or endogenous cognitive demands is diminished due to the transition into a subcritical state (see Fagerholm et al., 2015; but also see Yu et al., 2017, and Cocchi et al., 2017). Therefore, between two individuals initially performing equally well in a working memory and attention task, the person with higher *H* while performing the task is likely exhibiting more efficient information processing, as if performing an easier task despite the apparent equal performance. Such an advantage will eventually emerge as higher performance in the task, because efficient information processing facilitates any *additional* processes required for *improving* the execution of task (Figure 2). In other words, we propose that more scale-free brain activity accommodates cognitive resources for improving task performance, hence characterizing individual differences in practice effects.

# RESULTS

# Scale Invariance Predicts Task Improvements in the Dual N-Back Task

In Study 1, participants performed an audio-visual dual *n*-back (DNB) task (Jaeggi et al., 2008) two times and watched an intermission video in between the task as a break (N = 56). In this task, participants had to press a button if a number (1–9) they heard was the same as the number they heard *n* trials ago (n = 2 or 3). Simultaneously, participants saw a square move across a 3 × 3 grid, and they needed to press a different button if the square appeared in the same location as it did *n* trials ago (n = 2 or 3; see Methods). We assessed brain *H* and task improvement relationships to test our hypothesis that participants with higher *H* in their fMRI activity during rest and task runs would show greater improvements in DNB performance from the first run to the second run.

For each fMRI DNB task run, task performance was operationalized with a discrimination index A' averaged across all DNB task blocks (six blocks per run). There was an average improvement of  $\Delta A' = 0.045$ , t(55) = 7.50, p < .001 in performance (5.5% improvement) from



**Figure 2.** Hypothetical relationship between differences in fMRI Hurst exponent (*H*) and differences in task performance improvements with practice. The participant shown in red, whose brain activity is more scale-invariant when performing the task compared to their blue counterpart (left panel), is expected to improve their task performance to a greater degree than their counterpart (right panel).

first run of DNB (A' mean = 0.827, *SD* = 0.081) to second run of DNB (A' mean = 0.872, *SD* = 0.081), with large variability in the amount of change in performance ( $\Delta A'$ ) across individuals (*SD* = 0.045; Figure 3A). All performance levels (shown in Figure 3A) were above chance (A' > 0.5), suggesting that the participants were engaged and compliant during the DNB runs.

Across the three fMRI runs, the average whole-brain *H* (across the 268 brain parcels from Shen et al., 2013) was quantified for each participant and the values are plotted in Figure 3B. This average Hurst exponent across all brain parcels is henceforth referred to as  $H_{wb}$  (wb = whole brain). There is across-individual variability in the  $H_{wb}$  in both DNB task runs, but no overall mean difference between the two runs (mean = .684, *SD* = .046 for fist DNB; mean = .678, *SD* = .048 for second DNB; *t*(55) = 1.12, *p* = .267). The video run also showed across-individual variability in  $H_{wb}$  (mean = .725, *SD* = .052), with mean  $H_{wb}$  being significantly higher than the two task runs (*t*(55) = 6.44, *p* < .001 compared to first DNB and *t*(55) = 8.80, *p* < .001 compared to the second DNB). The higher  $H_{wb}$  for video watching compared to DNB tasks follow previous findings of widespread decreased *H* with increased task difficulty (Churchill et al., 2016; He, 2011; Kardan et al., 2020; Zhuang et al., 2022).

We then assessed how performance improvements (practice effects) are related to individual differences in scale-free brain dynamics. First, we looked at the relationship of  $H_{wb}$  with



**Figure 3.** (A) Performance on the dual *n*-back task (A') for all participants in the first and second runs of the DNB. Each line connects a participant's performance in the first run to their performance in the second run. (B) Average Hurst exponent (*H*) for all participants in the first DNB run, the video run, and the second DNB run. Each line connects a participant's average *H* across the runs. (C) Relationship of adjusted change in performance (adj.  $\Delta A'$ ) with the average *H* across participants in each of the three fMRI runs (dots are individual participants and each color is a separate run). The intercept of the regression of  $\Delta A'$  on initial performance (i.e., run1 A') is added to adj.  $\Delta A'$  in this figure to center the spread around the mean of adj.  $\Delta A'$  rather than zero. (D) The primary latent variable from behavioral partial least squares (PLS) relating adj.  $\Delta A'$  to parcel-wise *H* in the DNB experiment shows a predominantly positive *H* pattern that is significantly positively expressed in all imaging runs, that is, the first DNB run, the video run, and second DNB run. In the left panel, *y*-axis shows the correlation of the PLS weight with adj.  $\Delta A'$  at each run and error bars show 95% confidence intervals as indicated by bootstrapping: \**p* < .05, \*\**p* < .001. All red parcels in the right panel show bootstrap ratio Z<sub>BR</sub> values above +3 (total of five parcels) indicating a reliable positive association between *H* and the contrast in the left panel, i.e., higher *H* in those brain regions across all three brain imaging runs was related to greater performance improvements adjusting for baseline performance. There are no blue parcels with Z<sub>BR</sub> < -3, indicating an exclusively positive direction for the *H*-to-adj.  $\Delta A'$  association. Cross-block covariance ( $\sigma_{XY}$ ) shows the proportion of covariance between the left and right panel explained by this LV, and the *p* value is calculated from a permutation test for the eigenvalue for this LV.

performance change across participants from first to second DNB run. Importantly, we wanted to assess practice effects independent of baseline performance, so we regressed  $A'_0$  out of  $\Delta A'$  to make adj.  $\Delta A'$  scores that are linearly independent from baseline performance of the participants. In Figure 3C, the relationship between the  $H_{wb}$  in each run with the adj.  $\Delta A'$  scores across participants are shown with blue, orange, and yellow scatterplots for the first DNB, the video, and the second DNB runs, respectively. There were no significant correlations between the  $H_{wb}$  and performance improvement across participants, though all trends were positive (r = .019, p = .888 for  $H_{wb}$  during first DNB; r = .213, p = .115 for  $H_{wb}$  during video; r = .199, p = .142).

Second, we performed a multivariate analysis where H values were not averaged across the brain for each individual, but kept at parcel-wise level (268-node whole-brain gray matter atlas from Shen et al. [2013] spanning cortical, subcortical, and cerebellar regions). We conducted PLS regression analysis simultaneously relating H in all brain parcels from all three runs to the performance improvements across participants to find the multivariate pattern of parcel-wise H that maximally predicts tasks improvements in a data-driven manner. The primary latent variable from the PLS analysis (shown in Figure 3D) revealed an exclusively positive H pattern (five parcels with Z > +3 compared to no parcel with Z < -3; Figure 3D right panel) that are significantly correlated with higher task improvement (Figure 3D left panel). In DNB, higher H in five parcels, one located in right prefrontal, one in left prefrontal, one in right motor, one in left parietal and one in left cerebellum regions were reliably related to more task performance improvement. The threshold of  $\pm 3$  for bootstrap Z for statistical significance in the PLS brain latent variable was chosen the same as prior work (Kardan et al., 2019), but the positive gradient finding was consistent for less stringent threshold of Z = 2 (31 parcels with Z > +2 compared to no parcel with Z < -2). Together, the  $H_{wb}$  and the PLS results provide support for our hypothesis that higher H is related to more task performance improvement in the NDB task.

#### Scale Invariance Predicts Task Improvements in the N-Back Task

In Study 2, we tested if higher *H* was predictive of improvements in performance of the n-back task (NBK) from first run to second run in the Human Connectome Project (HCP) sample (N = 599). In this task participants were shown a series of images, and they had to indicate whether the current image matched the image shown *n* trials ago (n = 0 or 2).

The NBK performance in each run was operationalized as the response accuracy to the 2-back task across the task blocks (the other condition of the HCP n-back task is 0-back—essentially a target-detection task). Including the 0-back accuracy in the performance accuracy does not change the relationship between Hurst exponent and  $\Delta$  Accuracy or the PLS results. The performance levels of participants across the two runs are shown in Figure 4A. There was a significant average improvement in performance (8.6% improvement;  $\Delta$  accuracy = 0.071; *t*(598) = 21.3, *p* < .001) from the first run of NBK (mean = 0.823, *SD* = 0.104) to the second run (mean = 0.899, *SD* = 0.099), with relatively large variability across individuals in the amount of change in performance (*SD* = 0.082; Figure 4A).

The average whole-brain Hurst exponent ( $H_{wb}$ ) values in each NBK run are plotted in Figure 4B for all participants. Similar to the DNB results, there is across-individual variability in the  $H_{wb}$  in the NBK runs (mean = .795, SD = .050 for first NBK; mean = .804, SD = .049 for second NBK). We found an overall mean difference between the two NBK runs where  $H_{wb}$  was significantly higher for the second NBK (t(598) = 5.96, p < .001), which follows previous reports of increased fMRI H upon increased task familiarity (Churchill et al., 2016).



**Figure 4.** (A) Performance accuracy in the 2-back task for the HCP participants across the two NBK runs. Each line connects a participant's performance in the two runs. (B) Average Hurst exponent (*H*) for all participants in the two NBK runs. Each line connects a participant's average *H* across the runs. (C) Relationship of adjusted change in performance with their average *H* across participants in each of the two fMRI runs (dots are individual participants and each color is a separate run). The intercept of the regression of  $\Delta$  Acc. on initial performance (i.e., run1 Acc.) is added to adj.  $\Delta$  Acc in this figure to center the spread around the mean of adj.  $\Delta$  Acc rather than zero. (D) The primary latent variable from behavioral PLS relating adj.  $\Delta$  Accuracy to parcel-wise *H* in the NBK data shows a predominantly positive *H* pattern that is significantly positively expressed in the two runs. In the left panel, *y*-axis shows the correlation of the PLS weight at each run with adj.  $\Delta$  Accuracy and error bars show 95% confidence intervals as indicated by bootstrapping: \**p* < .05, \*\**p* < .001. All red parcels in the right panel (nine total) show bootstrap ratio Z<sub>BR</sub> values above +3 indicating reliable positive *H* association with the contrast in the left panel. There are no blue parcels with Z<sub>BR</sub> < -3, indicating exclusively positive direction for the *H*-to-adj.  $\Delta$  performance association. Cross-block covariance ( $\sigma_{XY}$ ) shows the proportion of covariance between the left and right panel explained by this LV, and the *p* value is calculated from permutation testing for the eigenvalue for this LV.

Next, we investigated how individual differences in scale-free brain dynamics were related to the performance changes from the first NBK to the second NBK run in two ways. First, we plotted the relationship of  $H_{wb}$  (which is averaged across all brain parcels) with performance change across participants from first to second NBK run, with the run 1 performance regressed out of the performance change. These relationships between the  $H_{wb}$  in each run with the adj.  $\Delta$  Accuracy scores across participants are shown with blue and orange scatterplots in Figure 4C. Similar to Study 1, we found small positive trends between the  $H_{wb}$  and performance improvement across participants, though the correlation for the second run was statistically significant even at this coarse whole-brain level of analysis (r = .078, p = .056 for  $H_{wb}$  during first NBK; r = .093, p = .023 for  $H_{wb}$  during second NBK run).

Second, we performed a PLS regression analysis to simultaneously relate *H* in all brain parcels from the NBK runs to the performance improvements across participants. As shown in Figure 4D, the primary latent variable from the PLS analysis revealed an exclusively positive *H* pattern (i.e., nine parcels with Z > +3 compared to no parcel with Z < -3; Figure 4D, right panel) that are significantly correlated with higher task improvement (Figure 4D, left panel). In NBK, the nine parcels in the latent variable were located in right and left parietal, right and left temporal, right and left cerebellum, left occipital (two parcels), and left subcortex regions. This positive direction was consistent at the threshold of Z = 2 (there were 48 parcels with Z > +2 compared to no parcels with Z < -2). Together, the NBK study results for both the  $H_{wb}$  and the multivariate analysis again shows that higher H is related to greater task improvement.

#### Scale Invariance Predicts Task Improvements in the Word Completion Task

In Study 3, we used a dataset with a completely different task than the DNB and NBK, again asking whether higher *H* is indicative of more task improvement. The study involved a sample of participants performing six consecutive runs of Choose-and-Solve Task (N = 44) that tested working memory and crystallized knowledge (CAST; Choe et al., 2019). Briefly, in this task<sup>1</sup> words with omitted letters were shown to the participant and they had to choose the right letter that would complete the word (see Methods).

For each of the six CAST (Choe et al., 2019) fMRI runs, task performance for a participant was quantified as their accuracy \* difficulty level of word completion questions they chose to solve (i.e., weighted accuracy scaled to 0-to-1 range; see Methods). Another difference between this dataset and those in Studies 1 and 2 was that difficulty of trials were tied to the performance of the participant. Each two consecutive correct responses would increase the difficulty of the following trials, and each two consecutive errors would decrease the difficulty of the following trials. The performance levels of participants across the six runs are shown in Figure 5C. There was no significant average improvement of task performance from the first run of CAST (mean = 0.451, *SD* = 0.196) to the last run (mean = 0.473, *SD* = 0.211). An ANOVA showed no performance difference across the six runs (*F*(5,258) = .417, *p* = .837), but there was large variability in the amount of change in performance ( $\Delta$  Accuracy from first run to sixth run) across individuals. In other words, some individuals showed improved performance while others showed worsened performance; *SD* = 0.301 (see spread across *y*-axis in Figure 5C).

The average whole-brain Hurst exponent ( $H_{wb}$ ) values are plotted in Figure 5B for all participants across the six CAST runs. Similar to the Studies 1 and 2 results, there is acrossindividual variability in the  $H_{wb}$  in all CAST runs but also a slight overall mean difference between the six runs (mean = .658, SD = .035 for first CAST; mean = .666, SD = .034 for second CAST; mean = .673, SD = .038 for third CAST; mean = .676, SD = .038 for fourth CAST; mean = .682, SD = .042 for fifth CAST; mean = .681, SD = .043 for sixth CAST; F(5,258) = 2.52, p = .030). The difference is driven by the last three runs having significantly higher  $H_{wb}$  compared to the first run (fourth run: t(43) = 3.13,  $p_{adj}$  = .047; fifth run: t(43) = 4.00,  $p_{adj}$  = .004; sixth run: t(43) = 3.46,  $p_{adj}$  = .019; p values are Bonferroni-adjusted for 15 pairwise comparisons). The higher H after task repetition follows previous reports of increased fMRI H upon increased task familiarity (Churchill et al., 2016) and our results in the Study 2 (HCP) dataset.

Next, we asked how performance changes from the first to the last CAST run are related to individual differences in scale-free brain dynamics. Similar to Study 1, we first investigated the relationship of  $H_{wb}$  with performance change across participants from first to sixth CAST run, with the run one performance regressed out of the performance change. In Figure 5C, the relationship between the  $H_{wb}$  in each run with the adj.  $\Delta$  Accuracy scores across participants are shown with scatterplots in different colors. Similar to Study 1, there were no significant correlations between the  $H_{wb}$  and performance improvement across participants, though all trends were positive (r = .116, p = .453 for  $H_{wb}$  during first CAST; r = .204, p = .184 for  $H_{wb}$  during second CAST; r = .143, p = .355; for  $H_{wb}$  during third CAST; r = .091, p = .556 for  $H_{wb}$  during

<sup>&</sup>lt;sup>1</sup> There is also a math equation completion component to this task that is not used in the current study.



**Figure 5.** (A) Performance on the word completion CAST for all participants across all six runs. Each line connects a participant's performance in the consecutive runs. (B) Average Hurst exponent (*H*) for all participants in the six CAST runs. Each line connects a participant's average *H* across the runs. (C) Relationship of adjusted change in performance with their average *H* across participants in each of the six fMRI runs (dots are individual participants and each color is a separate run). The intercept of the regression of  $\Delta$  Acc. on initial performance (i.e., run1 Acc.) is added to adj.  $\Delta$  Acc in this figure to center the spread around the mean of adj.  $\Delta$  Acc rather than zero. (D) The primary latent variable from Behavioral PLS relating adj.  $\Delta$  Accuracy to parcel-wise *H* in the CAST experiment shows a predominantly positive *H* pattern that is significantly positively expressed in all six runs, that is, higher H in those areas was related with improvements in performance. In the left panel, *y*-axis shows the correlation of the PLS weight at each run with adj.  $\Delta$  Accuracy and error bars show 95% confidence intervals as indicated by bootstrapping: \*p < .05, \*\*p < .001. All red parcels in the right panel (four total) show bootstrap ratio Z<sub>BR</sub> values above +3 indicating reliable positive *H* association with the contrast in the left panel. There are no blue parcels with Z<sub>BR</sub> < -3, indicating exclusively positive direction for the H-to-adj.  $\Delta$  performance association. Cross-block covariance ( $\sigma_{XY}$ ) shows the proportion of covariance between the left and right panel explained by this LV, and the *p* value is calculated from permutation tests for the eigenvalue for this LV.

fourth CAST; r = .061, p = .693 for  $H_{wb}$  during fifth CAST; r = .239, p = .118 for  $H_{wb}$  during sixth CAST run).

We then performed a PLS regression analysis to simultaneously relate *H* in all brain parcels from all six CAST runs to the performance improvements across participants from the first to the last run. The primary latent variable from the PLS analysis (shown in Figure 5D) again revealed an exclusively positive *H* pattern (i.e., four parcels with Z > +3 compared to no parcel with Z < -3, Figure 5D, right panel) that are significantly correlated with higher task improvement (Figure 5D, left panel). In CAST, higher *H* in four parcels, one located in left prefrontal, one in right motor, and two in the left temporal regions were reliably correlated with performance improvements in the task. At the less stringent threshold of Z = 2 there were 19 parcels with Z > +2 compared to 4 parcels with Z < -2). Together, the *H*<sub>wb</sub> and the PLS results again show that higher *H* is related to greater task improvement upon repetition in the CAST task.

#### Exploring the Stability of Spatial Patterns of H and Their Overlap Across Tasks

We performed some exploratory analyses to assess the stability of the spatial patterns of H in the PLS regressions, as well as their overlap across different tasks. These results are outlined below and detailed in the Supporting Information, sections 1–5.

**Overlap of parcel-wise** *H* **latent variables across datasets.** At the bootstrap ratio Z = 3, there were no overlapping parcels (from the 268 parcels of the Shen et al. [2013] parcellation) in the DNB, CAST, and NBK PLS latent variables (i.e., no overlap between parcels indicated in Figures 3D, 4D, and 5D). The lack of overlap was independent of specific Z threshold, as the nonthresholded primary brain PLS LVs across the three tasks were dissimilar ( $r_{1,2} = -.016$ , p = .792;  $r_{1,3} = .032$ , p = .611;  $r_{2,3} = -.176$ , p = .004, where 1, 2, and 3 indices refer to DNB, NBK, and CAST tasks, respectively). These exploratory results are discussed further in the Discussion section.

**Stability of parcel-wise** *H* **latent variables based on different analytic choices.** First, to assess the stability of the PLS results associating *H* in brain parcels to improvements in task performance, we repeated the analyses with a different whole-brain parcellation consisting of 392 parcels (Craddock et al., 2012). Across all three datasets, we found consistent PLS results with the Shen 268 version of the analysis where brain *H* positively loaded on higher task performance improvements. However, the stability of the spatial brain pattern was low to moderate (r = .375, p < .001 in DNB, r = .478, p < .001 in NBK, and r = .174, p < .001 in CAST). These results are detailed in the Supporting Information, section 1.

Next, to assess if differences in the temporal structures of tasks contributed to the reported findings, we recalculated the *H* exponents in the three datasets after regressing out the temporal block structure in each task run from the BOLD timeseries. We then repeated the PLS regressions relating adj.  $\Delta$  Accuracy to parcel-wise *H*. The spatial pattern in brain *H* latent variable was highly correlated with the original analysis in all three datasets (r > .952, p < .001). These results are detailed in the Supporting Information, section 2.

Finally, we repeated the PLS analyses using *H* estimated from Wavelet Leaders Multifractal method (Jaffard et al., 2006; Wendt et al., 2007) instead of detrended fluctuations analysis (DFA) to supplement our evaluation of linear fit of the *H* exponents (Supporting Information, section 3) to the fMRI data. This analysis is detailed in Supporting Information, section 4, and the PLS results showed medium to high correlation between the spatial patterns of *H* from the WLMF method compared to our DFA-based results shown in Figures 3-5 (r = .647, p < .001 for DNB; r = .757, p < .001 for NBK; and r = .473, p < .001 for CAST; see Supporting Information, section 4.1, for details).

**Comparing the mean** *H* **across tasks.** When comparing the mean *H* values between different tasks, we found that the NBK task from the HCP dataset had significantly higher  $H_{wb}$  compared to the task runs in DNB (two-sample *t*(653) = 18.4, *p* < .001) and CAST (two-sample *t*(641) = 17.8, *p* < .001) datasets. Additionally, as expected, the video run in the DNB study had significantly higher mean H compared to the DNB runs of the same participants (*t*(55) = 8.21, *p* < .001) or the CAST runs of other individuals from the same scanner (two-sample *t*(98) = 5.89, *p* < .001). These exploratory results are discussed further in the Discussion section.

# DISCUSSION

Criticality is a unifying and therefore appealing framework, as it allows for the description of the many ways in which information flows through the brain at different spatiotemporal scales (e.g., Scott et al., 2014). Previous work has theorized that the shift from resting-state nearcritical dynamics to a focused, task-induced subcritical state may be to switch from the advantage of higher dynamics range and state repertoire to a state of lower dynamic range that can reduce interference during task performance (Fagerholm et al., 2015). Importantly, the variability in *H* across individuals is comparable to the size of task-induced *H* suppression effects. Therefore, we think it is important to combine and compare state-like and trait-like *H* differences to better understand the relationship of *H* with cognitive performance. We hypothesized that the temporal and spatial efficiency of information transfer between the nodes of brain networks is diminished when *H* is low. Specifically, given the modulation of *H* with cognitive exertion (Churchill et al., 2016; Kardan et al., 2020; Zhuang et al., 2022), we hypothesized that between-individual differences in fMRI scale invariance when performing equally well on a task could signal differences in the potential for further improvement in task performance, as higher *H* may indicate the task is being performed more 'easily' and closer to a resting critical state.

Previous research has indicated trait-like patterns of higher *H* across participants being related to superior cognitive performance (Ouyang et al., 2020; Stier et al., 2023; Suckling et al., 2008; Zhuang et al., 2022). Here we explored a more nuanced topic: whether higher trait *H* at baseline would predict improvements in task performance with practice, which combines elements of state and trait factors. Across three datasets with different cognitive tasks, differences in scale-free dynamics of the BOLD signal were reliably associated with cognitive task improvement with higher *H* values being related to improved behavioral performance. Patterns of higher *H* of fMRI activity were significantly associated with more task improvement, even when adjusting for baseline task performance, in DNB, CAST, and NBK tasks. Taken together, our findings provide evidence for our hypothesis that more scale-free brain activity accommodates cognitive resources for improving task performance.

We also compared the differences in mean H across the three different studies. These results are tempered by differences in signal-to-noise ratio (SNR) across fMRI datasets that could originate from different scanners, which are known to impact H (Meisel et al., 2017a). The NBK task from the HCP dataset had significantly higher  $H_{wb}$  compared to the task runs in DNB and CAST datasets. This is expected from previous studies showing H is suppressed more with more difficult tasks (Churchill et al., 2016; Kardan et al., 2020), as the NBK data consisted of 0-back and 2-back task blocks, both of which are considerably easier than the dual 2-back and dual 3-back in the DNB dataset and the word completion task in the CAST dataset. As expected, the video run in the DNB study had significantly higher mean H compared to the DNB runs of the same or the CAST runs of other individuals from the same scanner. However, it should be mentioned that scanner, image acquisition, SNR, and some preprocessing differences between the HCP dataset and the DNB and CAST datasets (which were collected using the same scanner) may be related to the mean H values as well. For example, the videowatching run in the DNB dataset still has lower mean H compared to the HCP dataset's NBK task (two-sample t(653) = 11.4, p < .001). One possibility for this could be due to the delay of fMRI scale-free dynamics in returning to baseline H after performing a task, as the video-watching run in the DNB study occurs shortly after the first DNB task (e.g., Barnes et al. [2009] report  $\sim$ 6 min delay of fMRI H to recover to rest levels after a 2-back task).

One question is whether these differences in *H* reflect state-based or trait-based factors with respect to differences in practice effects. The state-based interpretation of these data is that individuals who were in a higher *H* state at the time of the experiment processed the tasks more efficiently, leaving cognitive resources available for *additional* learning of task characteristics and forming better task-relevant memories and cognitive strategies. The higher state of *H* could be due to, for example, lower stress or fatigue (Churchill et al., 2015). The additional encoding of task-relevant information then enabled these individuals to perform better the second time around.

20wnloaded from http://direct.mit.edu/netn/article-pdf/7/3/1129/2154/754/netn\_a\_00319.pdf by HONG KONG POLYTECHNIC UNIVERSITY user on 24 April 2024

The trait-based interpretation of these data/results can be made in two related, but not equivalent ways. Both relate to individual differences in an unobserved trait such as fluid intelligence and/or white matter (WM) capacity. The first interpretation assumes no direct relationship between H and trait WM/IQ absent from cognitive load. Under this account, the tasks utilized here demanded less cognitive effort from task improvers due to them having higher fluid intelligence or working memory capacity, which is in line with the neural efficiency intelligence hypothesis (Neubauer & Fink, 2009a, 2009b). The lower amount of exerted effort then led to less suppression of H (Barnes et al., 2009; Kardan et al., 2020). This means that lower H during tasks for participants whose performance did not improve (or decreased) is a proxy for their amount of cognitive exertion, which is high, and therefore they are not able to improve due to their WM capacity limitations. As such, higher or lower H is not a cause for more or less performance improvements, but a consequence of individuals being in different states of cognitive effort exertion.

The second trait-based interpretation assumes a direct and rigid relationship between H and WM capacity/IQ at all times. In other words, participants whose performance improved more may have a more critically organized functional brain network dynamics at baseline due to trait-level characteristics (e.g., higher WM capacity or IQ). These individuals then have consistently higher H than others, even when not performing a task (e.g., during the videowatching runs in the DNB study). Their higher H during cognitive tasks then enable them to more readily improve their performance due to advantages of criticality discussed before (He, 2011; Kitzbichler et al., 2009; Proekt et al., 2012). Based on this account, we may expect the same spatial brain patterns of higher H to reflect the high-performance trait across the individuals regardless of the task. However, the involved brain regions in the PLS latent variable from the DNB task and those in the PLS for NBK or CAST are not overlapping. We compared the PLS loadings on the parcel-wise brain H values across the DNB, CAST, and NBK tasks to determine if these positive H patterns that are predictive of performance improvements were consistent across the tasks. We found that the spatial patterns of H related to higher performance improvement in DNB, CAST, and NBK tasks were dissimilar. This suggests that unlike the consistent direction of [higher H]  $\rightarrow$  [more performance improvement] across the tasks, the predictive H<sup>↑</sup> features (i.e., brain regions) are not task-general, though it is not clear if the patterns are specific to task demands or noisy in any one dataset.

In addition to contributions to the criticality framework and theory, our findings also have practical implications. Specifically, previous clinical research has proposed that variation in practice effects provide unique diagnostic and treatment information for clinical populations. For example, older adults that show the expected practice effects in a test respond more to treatment for cognitive decline than those that do not show practice effects (Calero & Navarro, 2007; Duff et al., 2010; Fiszdon et al., 2006; Sergi et al., 2005; Watzke et al., 2008). However, the same line of research has found individual differences in practice effects for many cognitive tests to be uncorrelated with a wide range of demographic and cognitive ability scales that typically influence cognitive scores themselves (Duff et al., 2012; but also see Calamia et al., 2012). Our results suggest that *H* provides a promising avenue for future research in this field, as higher *H* was indicative of performance improvements across different tasks irrespective of initial task performance at baseline (see also Supporting Information, section 5).

There are a number of limitations to our study. First, it is important to consider alternative processes unrelated to criticality that may yield power law scaling in empirical brain data (see Cocchi et al., 2017; Farmer, 2015). This is particularly challenging to assess in the relatively narrow-band fMRI data where, in addition to being inherently slow, drift and physiological

noise are filtered out, thus restricting the temporal scales to fewer than two orders of magnitude (roughly .01 to .1 Hz; see Cocchi et al., 2017). Additionally, when hypothesizing about potential benefits of higher brain H for improvements in task performance, we considered the findings from Fagerholm et al. (2015). In this simultaneous EEG and fMRI study, Fagerholm et al. posited that shifts toward a subcritical brain state occur when the participants are sustaining attention to the task compared to rest. However, in a potential challenge to this view, Yu et al. (2017) hypothesized that activity during cognitive processing still exhibits power law scaling and that the apparent shift to subcriticality could be a result of unaccounted for changes in firing rate rather than changes in dynamic range. Second, as we mentioned, distinguishing state- versus trait-based contributions to individual differences in practice effects is difficult in the current study. Future studies should investigate the state versus trait components of between-subjects variability in H by assessing it across multiple days of testing in both resting-state and task runs. Third, the spatial patterns of H (i.e., the brain regions involved) were strictly data-driven and showed low to moderate stability with regards to the brain parcellations used (stability was moderate to high for other sensitivity analyses outlined in the Results' section Exploring the Stability of Spatial Patterns of H and Their Overlap Across Tasks and detailed in the Supporting Information results' sections 1-4). Future studies can interrogate the degree to which H predictors of changes in performance vary specifically with different cognitive tasks or share common nodes.

In conclusion, the current study investigated the relationship between differences in practice-based improvements in cognitive task performance with respondents' level of scale-free BOLD activity. Across three groups of participants performing different tasks, we found that individuals with higher fMRI H at the time of cognitive tests were more likely to improve their task performance when repeating the same cognitive task. Importantly, this was true even when controlling for baseline task performance, meaning that H provides predictive power for individual differences in practice effects above and beyond baseline behavioral performance. In addition, while building upon previous work relating brain scale invariance with overall behavioral performance, these results are the first to show how measures of fMRI scale invariance relate to changes in behavioral performance. These results provide empirical support for the hypothesis that brain networks impart functional advantages when their activity is in a more scale-free state. We propose that individual variability in Hacross the brain may hold promise as a neuronal marker of learning potential, which has wide-ranging theoretical and applied implications for cognitive neuroscience.

# **METHODS**

# Study 1: Dual N-Back Task (DNB) Dataset

Participants and procedure. In Study 1, we recruited 68 participants (41 female) aged between 18 and 40 years old (mean = 24.3 years, SD = 5.6 years). Twelve participants were excluded from analysis due to the following reasons: two participants were excluded due to incomplete fMRI data because of discomfort before the scanning session was finished; two were excluded due to technical issues with audio/visual during a run; five were flagged for sleepiness during the data acquisition as indicated by their eye-movement behavior by two on-site researchers (eye movements were monitored using an MR-compatible EyeLink 1000 system); and five were excluded after the primary data quality check (see fMRI Data Acquisition and Preprocessing sections). Our final sample was N = 56. All participants had self-reported normal or corrected-to-normal visual acuity and normal color vision. All participants provided their written informed consent as approved by the University of Chicago Institutional Review Board and were compensated \$35 for participation plus a potential bonus of \$10. Participants were informed before the scanning session that if they "stayed attentive and still" during scans they would receive a \$10 bonus. All participants who were not excluded based on the stated criteria above successfully received the bonus.

Following the collection of anatomical scans, three functional runs were acquired: a 7-min DNB run, a 10-min passive video-watching run, and a second 7-min DNB run. Participants were randomly assigned to passively watch one of two videos during the video run: a video of nonnature tourist attractions in Europe or a video of outdoor nature scenes. Videos were roughly equated for aesthetic preference as rated by a different sample of 30 participants prior to this study (Likert scale 1–7,  $M_{nature} = 5.47$ , SD = 1.14 and  $M_{urban} = 4.77$ , SD = 1.38), and did not include sound. After the scan session, participants were asked to give a preference rating (1–7 scale) for the video they watched. Ratings were included in subsequent analyses as a potential nuisance variable. At the beginning of each DNB run, participants were instructed to perform the task to the best of their ability. Linear regression of  $\Delta A'$  on video type (i.e., nature vs. urban) and preference rating for the video failed to find a significant relationship between video type or video rating and change in performance (t = 0.403, p = 0.688 for video type and t = -0.870, p = 0.388 for preference rating). Therefore, we collapsed the participants on the video types for the rest of the analyses.

**Task.** In an *n*-back task, participants are instructed to press a button if the current visual or auditory stimulus matches the stimulus that was presented '*n*' previous trials back. The dual *n*-back (DNB) is a variant of this task in which two stimuli are presented simultaneously. Here, these stimuli were spoken integers, 1–9, and a blue square whose position varied in a  $3 \times 3$  grid (see Figure 5). The paradigm was implemented in MATLAB and its code is publicly available at https://enl.uchicago.edu/stimuli-software/ (Layden, 2018).

On each trial of the DNB task, participants pressed their right index finger, right middle finger, both fingers, or neither finger, to indicate a position match, a number match, both a position and number match, or no match. Each trial lasted 3,000 ms, and the button press was permitted throughout the trial. Immediate feedback was provided to participants via red (incorrect press) or green (correct press) text at the bottom of the screen (see Figure 6).

Each functional MRI run included six blocks of the DNB task (four 2-back blocks and two 3-back blocks). Each block contained 20 + n trials (n = 2 or 3), resulting in a total of 134 trials per DNB fMRI run. Blocks were separated by a 10-s countdown that indicated whether the upcoming task would be 2-back or 3-back. As in the practice, the discrimination index A' (Stanislaw & Todorov, 1999) was used as the main performance measure. A' is similar to other sensitivity indices such as d', but is more robust to nonnormality of responses (Stanislaw & Todorov, 1999). Furthermore, unlike d', A' = 0.5 corresponds to chance level performance, A' = 1 corresponds to perfect performance, and A' < 0.5 corresponds to performance that is systematically worse than chance. A' is calculated as follows:

$$A' = 0.5 + sign \frac{(Hit - FA) * [(Hit - FA)^2 + |(Hit - FA)|]}{(4 * max(Hit, FA) - 4 * Hit * FA)}$$

where *Hit* is the number of correct button presses and *FA* is the number of false alarms for both numbers and positions in a task block, where sign(Hit - FA) equals: +1 if (Hit - FA) > 0, 0 if (Hit - FA) = 0, and -1 if (Hit - FA) < 0, and where max(Hit, FA) equals the bigger value between *Hit* and *FA*.

Adjusted  $\Delta A'$ . Consider  $y = (A'_2 - A'_1)$  and X = a matrix containing ones in the first column and  $A'_1$  in the second column (i.e., A' from the first run of the task). Then adj.  $\Delta A'$  was the

Downloaded from http://direct.mit.edu/netn/article-pdf/7/3/1129/2154754/netn\_a\_00319.pdf by HONG KONG POLYTECHNIC UNIVERSITY user on 24 April 2024



**Figure 6.** Audio-visual dual *n*-back task paradigm. In this example of the first three trials in a dual 2-back round, the participant correctly pressed their index finger for a match between the current and 2-back position of blue square, but falsely pressed their middle finger when they should not have (i.e., 2 does not match 9; so the correct response was only an index finger response and not an index finger and middle finger response). This is an example of one hit and one false alarm.

residual of regression of y on X: adj.  $\Delta A' = y - X\hat{\beta}$ , where:  $\hat{\beta} = (X'X)^{-1}X'y$  is the coefficients of the least squares fit of y on X.

### Study 2: N-Back Task (NBK) Dataset

**Participants.** In Study 2, we analyzed data from the Human Connectome Project (HCP) release S1200, a multisite consortium that collected MRI, behavioral, and demographic data from 1,113 participants (final N = 599 after scan exclusions based on head motion and quality control).

**Task.** The *n*-back task in the HCP dataset (Barch et al., 2013) includes two runs of eight blocks each with 10 trials in each block. A picture is shown in every trial and participants are instructed to press a button for every picture. If the currently presented picture matches thecued picture (0-back, four blocks in each run) or the same picture that was presented two pictures before (2-back, four blocks in each run), participants press one button with their right index finger. For nonmatching pictures, participants press a second button with their right middle finger. At the start of each block, a 2.5-s cue indicates the task type ("2-back" or "target=" and a photo of the target stimulus).

Two blocks of 0-back and two blocks of 2-back contain tools (one in each run), another two in each task contain body parts, another two contain neutral faces, and another two contain places. There are 24 unique stimuli per type presented in separate blocks, each trial is 2.5 s (2 s-presentation of a stimulus, followed immediately by a 500-ms fixation cross) resulting in 160 total trials in 16 blocks of *n*-back. Four fixation blocks (15 s each) also occur in each run after every other *n*-back block. Accuracy in each run was calculated as the proportion of correct responses in the 2-back trials across the four 2-back blocks of the run.

Adjusted  $\Delta$  Accuracy. Consider  $y = (Acc_2 - Acc_1)$  and X = a matrix containing ones in the first column and accuracy in the first run (Acc<sub>1</sub>) in the second column. Then adj.  $\Delta$  Acc was the

residual of regression of y on X: adj.  $\Delta A' = y - X \hat{\beta}$ , where  $\hat{\beta}$  is the coefficients of the least squares fit of y on X:  $\hat{\beta} = (X'X)^{-1}X'y$ .

#### Study 3: Word Completion Task (CAST) Dataset

**Participants.** In Study 3, an independent sample of subjects from the same site as Study 1 was provided by Choe et al., (2019). This dataset consists of fMRI runs for 49 participants aged between 18–35 (final N = 44 after scan exclusions based on head motion and quality control). All participants provided their written informed consent as approved by the University of Chicago Institutional Review Board.

**Task.** Participants performed a math and word Choose-and-Solve Task (CAST) for 6 minutes in every run. The fMRI acquisition parameters and preprocessing pipeline were the same as in Study 1. CAST involves choosing to solve math equation completion and word completion tasks and is originally designed for detecting math anxiety and math avoidance behavior (Choe et al., 2019). The participants performed the CAST in six runs in fMRI scanner, which provided us with a different learning/practice paradigm to complement the DNB study. The questions were designated as having a 1–7 difficulty level (Choe et al., 2019). The performance of participants in CAST was quantified as their accuracy \* difficulty level of questions they solved, since the question difficulty was adaptive in a manner that two correct answers in a row would result in an increase in difficulty and one wrong answer would result in decrease in question difficulty. Because the number of trials where difficult math questions (with higher reward) were chosen over easy math questions (with lower reward) was very sparse across participants, performance was quantified only over word completion trials.

In word completion trials, participants see words with omitted letters replaced by  $\sim$  and  $\Box$  characters. The participant has to quickly choose (<2,000 ms) the correct letter that should be in the square (i.e.,  $\Box$ ). For example, for E  $\sim \Box$ DE  $\sim$  CE, the correct choice is letter 'l' (the word is 'evidence').

Adjusted  $\Delta$  Accuracy. Similar to the other tasks, we regressed out accuracy in run one out of the change in accuracy to construct adj.  $\Delta$  Acc for CAST. Specifically, if  $y = (Acc_6 - Acc_1)$  and X = a matrix containing ones in the first column and accuracy in the first run (Acc<sub>1</sub>) in the second column, then adj.  $\Delta$  Acc was the residual of regression of y on X: adj.  $\Delta A' = y - X \hat{\beta}$ , where  $\hat{\beta}$  is the coefficients of the least squares fit of y on X:  $\hat{\beta} = (X'X)^{-1}X'y$ .

### fMRI Data Acquisition and Preprocessing for Studies 1 and 3

Images were acquired on a Philips Achieva 3.0 T scanner with a standard quadrature 32channel head coil at University of Chicago MRI Research Center. A T1-weighted gradient echo (MP-RAGE) was used to acquire high-resolution anatomical images for each participant (TR = 8 ms, TE = 3.5 ms, flip angle = 8°, FOV = 240 mm × 228 mm × 171 mm, matrix size = 240 × 228, in-plane resolution 1.0 mm<sup>2</sup>, slice thickness = 1.0 mm, 171 sagittal slices). Functional T2\* weighted images were acquired using an echo-planar sequence (TR = 2,000 ms, TE = 26 ms, flip angle = 77°, FOV = 208 mm × 208 mm × 143.25 mm, matrix size = 64 × 64, in-plane resolution 3.25 mm<sup>2</sup>, slice thickness = 3.25 mm with 0.25-mm gap, 41 transverseoblique slices parallel to the A-P line) during the DNB runs (241 volumes for each run) and the video run (305 volumes).

Initial data quality checks were performed using MRIQC (Esteban et al., 2017), which revealed excessive head movement and low tSNR (peak frame displacement > 2 mm, mean frame displacement > 0.2 mm, or tSNR < 50) for five participants during at least one of the

scanning runs. These participants were excluded from analysis. The first five volumes of each functional run were discarded for all participants.

The preprocessing was performed using FMRIPREP version 1.5.0 (Esteban et al., 2019), a Nipype (Gorgolewski et al., 2011) based tool. Each T1w (T1-weighted) volume was corrected for INU (intensity nonuniformity) using N4BiasFieldCorrection v2.1.0 and skull-stripped using antsBrainExtraction.sh v2.1.0 (using the OASIS template). Spatial normalization to the ICBM 152 Nonlinear Asymmetrical template version 2009c was performed through nonlinear registration with the antsRegistration tool of ANTs v2.1.0 (Avants et al., 2009), using brain-extracted versions of both T1w volume and template. Brain tissue segmentation of cerebrospinal fluid (CSF), white matter (WM), and gray matter (GM) was performed on the brain-extracted T1w using fast (FSL v5.0.9).

Functional data was motion corrected using mcflirt (FSL v5.0.9). "Fieldmap-less" distortion correction was performed by coregistering the functional image to the same-subject T1w image with intensity inverted constrained with an average field-map template, implemented with antsRegistration (ANTs). This was followed by coregistration to the corresponding T1w using boundary-based registration with six degrees of freedom, using flirt (FSL). Motion correcting transformations, field distortion correcting warp, BOLD-to-T1w transformation, and T1w-to-template (MNI) warp were concatenated and applied in a single step using antsApply-Transforms (ANTs v2.1.0) using Lanczos interpolation.

Frame-wise displacement (Power et al., 2012) was calculated for each functional run using the implementation of Nipype. Following Power et al. (2014), we performed a 36-parameter confound regression that included the time courses of mean CSF signal, mean global signal, mean WM signal, the six standard affine motion parameters (x, y, z, pitch, roll, and yaw), their squares, their derivatives, and their squared derivatives of these signals. We also simultaneously regressed out linear and quadratic trends to remove drift related signals. This was followed by the application of a band-pass filter with a high-pass cutoff of .008 Hz and a low-pass cutoff of .12 Hz via the 3dBandpass command in AFNI.

After preprocessing, the whole brain was parcellated by applying a 268-node whole-brain GM atlas spanning cortical, subcortical, and cerebellar regions (Shen et al., 2013). fMRI data acquisition and preprocessing for Study 3 was the same as Study 1. Six of the 268 parcels had significant signal dropout in nine of the participants and were excluded from further analyses to preserve sample size. The fMRI signal time course in each run was averaged across brain voxels within each of the 262 nodes (i.e., brain parcels), and *H* was estimated in each parcel for all the runs in each participant.

### fMRI Data Acquisition and Preprocessing for Study 2

In Study 2, we analyzed data from the HCP release S1200. We downloaded the minimally preprocessed, open-access *n*-back fMRI data from connectomeDB (https://db .humanconnectome.org/). The details of the acquisition parameters and prepossessing of these data can be found in Glasser et al. (2013), and the additional p reprocessing steps to the minimally preprocessed data are the same as Kardan et al. (2022). Briefly, preprocessing for task data included gradient nonlinearity distortion correction, field-map distortion correction, realignment, and transformation to a standard space. In addition, we applied additional preprocessing steps to the minimally preprocessed task data. This included a high-pass filter of 0.001 Hz, via fslmaths (Jenkinson et al., 2012), and the application of the ICA-FIX denoising procedure using the HCPpipelines (https://github.com/Washington-University/HCPpipelines) tool, which regresses out nuisance noise components effectively, similar to regressing out

motion parameters and tissue type regressors (Parkes et al., 2018). The cleaned volumetric BOLD images were spatially averaged into 268 predefined parcels (Shen et al., 2013) similar to Studies 1 and 3.

For participants to be included in the Study 3 analyses, both of their *n*-back fMRI runs had to have low head motion (mean FD < 0.2 mm and max FD < 2 mm similar to the DNB and CAST datasets). Additionally, we removed participants with any quality control flags from the HCP quality control process (variable QC\_Issue), in either of their *n*-back fMRI runs, resulting in a final sample of N = 599 participants.

#### Estimation of Scale-Free Activity (H)

Following our hypothesis, to evaluate the degree of scale-free dynamics of BOLD and its relationship to practice effects between individuals, we estimated the Hurst exponent (H) of the fMRI time series from all three functional runs in for each participant (i.e., DNB-1, video watching and DNB-2). There are many different methods to estimate H. Here we used both DFA and wavelet leader multifractal (WLMF) formalisms, both of which are robust to signal nonstationary and low-frequency confounds (Churchill et al., 2016; Hardstone et al., 2012; Jaffard et al., 2006; Peng et al., 1995). The estimations were done on a parcel-wise level, and the DFA estimations of H were highly correlated with the first-order cumulant (i.e., mono-fractal) estimations of H from the WLMF. As such, further analysis was carried out using the DFA estimates, as this method is more computationally efficient.

To elaborate DFA, consider the linearly detrended BOLD timeseries x(t) in a parcel over a run of total length *T*. There are three runs in the DNB study (the first dual *n*-back run, the video run, and the second dual *n*-back run), with the task runs including three blocks of dual 2-back and three blocks of dual 3-back each. In the HCP dataset there are two runs of the *n*-back task (each containing four blocks of 0-back and four blocks of 2-back). Finally, in the CAST dataset there are six runs of the choose-and-solve word completion task containing 20 blocks in total. This signal is first integrated and transformed into a cumulative sum y(t), where  $y(t) = \sum_{i=1}^{t} (x(i) - x_{ave})$ ; t = 1, ..., T. x(i) is the *i*th data point in the time series and  $x_{ave}$  is the average amplitude over all of the time series. Next, y(t) is divided into windows of equal length *n*. A least-square linear regression is fit to each subdivision of y(t) with length *n*, with the fitted values denoted as  $\hat{y}_n(t)$ . Next, we detrend the integrated time series y(t) by subtracting the local trend (i.e., the local least squares straight-line fit)  $\hat{y}_n(t)$  in each window. The root-mean-square magnitude of fluctuations on the detrended data F(n) is then computed over a range of window sizes:

$$F(n) = \sqrt{\frac{1}{T} \sum_{t=1}^{T} [y(t) - \hat{y}_n(t)]^2}$$

were n = 50 TRs is maximum window size corresponding to 0.01 Hz minimum frequency in the current study, and n = 3 TRs is minimum window size for fitting a line with a nonzero residual. Finally, the linear fit of log(n) versus log(F(n)) is calculated, and the slope of this fitted line is used as the estimate of the degree of scale invariance (*H*) for the parcel time series x(t). A slope of H = 0.5 indicates no long-range correlation in the signal (i.e., a random walk), while *H* values closer to 1 indicate greater scale invariance.

### Partial Least Squares Analysis

Multivariate methods applied to fMRI data offer a novel opportunity to discover meaningful associations between distributed patterns of brain activities and behavioral measures across

runs in a single statistical model (e.g., Kardan et al., 2019, 2020), as opposed to univariate methods where conditions are regressed on every cluster of voxels separately. PLS (Krishnan et al., 2011; McIntosh & Lobaugh, 2004) analysis was used to identify the relationship between the set of parcel-wise *H* values with group-by-run treatment levels. The PLS implementation software was downloaded from Randy McIntosh's lab at https://www.rotman-baycrest.on.ca/index.php?section=84. In PLS, the goal of the analysis is to find weighted patterns of the original variables in the two sets (termed "latent variables" or "LVs") that maximally covary with one another. Briefly, PLS is computed via singular value decomposition (SVD). The covariance between the two data sets *X* (parcel-wise *H* values across runs) and *Y* (continuous  $\Delta$  Accuracy values) is computed (*X'Y*) and is subjected to the SVD:

### SVD(X'Y) = USV'

where *U* and *V* (the right and left singular vectors) provide weights (or "saliences") for the two sets (parcel-wise *H* across runs and  $\Delta$  Accuracy), respectively. The scalar singular value on the diagonal matrix *S* is proportional to the "cross-block covariance" between *X* and *Y* captured by the LV, and is naturally interpreted as the effect size of this statistical association (reported as  $\sigma_{XY}$ ). Additionally, we corelated the U scores with the V scores in each PLS latent variable to calculate the pseudo  $R^2$  in that LV.

In our study, a set of 1,000 covariance matrices were generated by randomly permuting condition labels for the *X* variables (brain set). These covariance matrices embody the null hypothesis that there is no relationship between *X* and *Y* variables. They were subjected to SVD resulting in a null distribution of singular values. The significance of the original LV was assessed with respect to this null distribution. The *p* value was estimated as the proportion of the permuted singular values that exceed the original singular value.

Bootstrapping was used to determine the reliability with which each parcel's H contributes to the overall multivariate pattern. A set of 5,000 bootstrap samples were created by resampling subjects with replacement within each run (i.e., preserving  $\Delta$  Accuracy values). Each new covariance matrix was subjected to SVD as before, and the singular vector weights from the resampled data were used to build a sampling distribution of the saliences from the original data set. The purpose of a constructed bootstrapped sampling distribution is to determine the reliability of each salience (i.e., saliences that are highly dependent on which participants are included in the analysis will have wide distributions). For the brain parcels, a single index of reliability (termed "bootstrap" ratio, or "Z" value) was calculated by taking the ratio of the salience to its bootstrap estimated standard error. A Z for a given connection is large when the connection has a large salience (i.e., makes a strong contribution to the LV) and when the bootstrap estimated standard error is small (i.e., the salience is stable across many resamplings). Here, parcels with Z > 3 or Z < -3 (equivalent to  $p \sim 0.0025$ , two-tailed, under normal distribution assumptions) were selected as showing reliable H relationship to  $\Delta$  Accuracy, similar to Kardan et al. (2019, 2022). However, we also assessed Z > 2 or Z < -2 threshold ( $p \sim$ 0.05) to assess whether *positive* associations were dominant for less conservative thresholds.

#### **DATA SHARING STATEMENT**

The curated data (fMRI parcel-wise Hurst exponent matrices and behavioral measures) for all participants in the three studies will be made available on Open Science Framework upon publication here: https://osf.io/zsxfj. Raw data for Studies 1 and 3 can be requested from bermanm@uchicago.edu. The Human Connectome Project dataset (used in Study 2) is available at https://db.humanconnectome.org. Scripts to produce the results and figures in the

manuscript will be available on Github upon publication here: https://github.com/okardan /Practice\_Hurst.

# ACKNOWLEDGMENTS

Resources provided by the University of Chicago Research Computing Center, and an internal grant from University of Chicago to Marc G. Berman.

# SUPPORTING INFORMATION

Supporting information for this article is available at https://doi.org/10.1162/netn\_a\_00319.

# **AUTHOR CONTRIBUTIONS**

Omid Kardan: Conceptualization; Data curation; Formal analysis; Methodology; Visualization; Writing – original draft; Writing – review & editing. Andrew J. Stier: Methodology; Software; Writing – review & editing. Elliot A. Layden: Methodology; Writing – review & editing. Kyoung Whan Choe: Data curation; Methodology; Writing – review & editing. Muxuan Lyu: Data curation; Writing – review & editing. Xihan Zhang: Methodology; Writing – review & editing. Sian L. Beilock: Funding acquisition; Writing – review & editing. Monica D. Rosenberg: Methodology; Writing – review & editing. Marc G. Berman: Conceptualization; Funding acquisition; Investigation; Supervision; Writing – review & editing.

# FUNDING INFORMATION

Marc G. Berman, National Science Foundation (https://dx.doi.org/10.13039/100000001), Award ID: BCS-1632445. Marc G. Berman, TKF Foundation. Omid Kardan was supported by National Institute on Alcohol Abuse and Alcoholism T32 AA007477. This work was supported in part by a Grossman Institute for Neuroscience, Quantitative Biology, and Human Behavior from the University of Chicago (Pilot MRI Award to Marc G. Berman and Sian L. Beilock; Shared Equipment Award to Marc G. Berman).

# REFERENCES

- Arviv, O., Goldstein, A., & Shriki, O. (2015). Near-critical dynamics in stimulus-evoked activity of the human brain and its relation to spontaneous resting-state Activity. *Journal of Neuroscience*, 35(41), 13927–13942. https://doi.org/10.1523/JNEUROSCI .0477-15.2015, PubMed: 26468194
- Avants, B. B., Tustison, N., & Song, G. (2009). Advanced normalization tools (ANTS). *Insight Journal*, *2*, 1–35. https://doi.org/10 .54294/uvnhin
- Awh, E., & Jonides, J. (2001). Overlapping mechanisms of attention and spatial working memory. *Trends in Cognitive Sciences*, *5*(3), 119–126. https://doi.org/10.1016/S1364-6613(00)01593-X, PubMed: 11239812
- Bak, P., Tang, C., & Wiesenfeld, K. (1987). Self-organized criticality: An explanation of the 1/f noise. *Physical Review Letters*, 59, 381–384. https://doi.org/10.1103/PhysRevLett.59.381, PubMed: 10035754
- Barch, D. M., Burgess, G. C., Harms, M. P., Petersen, S. E., Schlaggar,B. L., Corbetta, M., ... Van Essen, D. C. (2013). Function in the human connectome: Task-fMRI and individual differences in

behavior. *NeuroImage, 80,* 169–189. https://doi.org/10.1016/j .neuroimage.2013.05.033, PubMed: 23684877

- Barnes, A., Bullmore, E. T., & Suckling, J. (2009). Endogenous human brain dynamics recover slowly following cognitive effort. *PLoS One*, *4*(8), e6626. https://doi.org/10.1371/journal.pone .0006626, PubMed: 19680553
- Beggs, J. M., & Timme, N. (2012). Being critical of criticality in the brain. *Frontiers in Physiology*, *3*, 163. https://doi.org/10.3389 /fphys.2012.00163, PubMed: 22701101
- Boedecker, J., Obst, O., Lizier, J. T., Mayer, N. M., & Asada, M. (2012). Information processing in echo state networks at the edge of chaos. *Theory in Biosciences*, *131*(3), 205–213. https://doi.org/10.1007/s12064-011-0146-8, PubMed: 22147532
- Calamia, M., Markon, K., & Tranel, D. (2012). Scoring higher the second time around: Meta-analyses of practice effects in neuropsychological assessment. *The Clinical Neuropsychologist*, *26*(4), 543–570. https://doi.org/10.1080/13854046.2012 .680913, PubMed: 22540222

- Calero, M. D., & Navarro, E. (2007). Cognitive plasticity as a modulating variable on the effects of memory training in elderly persons. *Archives of Clinical Neuropsychology, 22*(1), 63–72. https://doi.org /10.1016/j.acn.2006.06.020, PubMed: 17158023
- Chaudhuri, R., Knoblauch, K., Gariel, M.-A., Kennedy, H., & Wang, X.-J. (2015). A large-scale circuit mechanism for hierarchical dynamical processing in the primate cortex. *Neuron*, *88*, 419–431. https://doi.org/10.1016/j.neuron.2015.09.008, PubMed: 26439530
- Chialvo, D. R. (2004). Critical brain networks. *Physica A: Statistical Mechanics and Its Applications, 340*(4), 756–765. https://doi.org /10.1016/j.physa.2004.05.064
- Chialvo, D. R. (2010). Emergent complex neural dynamics. *Nature Physics*, *6*(10), 744–750. https://doi.org/10.1038/nphys1803
- Choe, K. W., Jenifer, J. B., Rozek, C. S., Berman, M. G., & Beilock, S. L. (2019). Calculated avoidance: Math anxiety predicts math avoidance in effort-based decision-making. *Science Advances*, 5(11), eaay1062. https://doi.org/10.1126/sciadv.aay1062, PubMed: 31799398
- Churchill, N. W., Cimprich, B., Askren, M. K., Reuter-Lorenz, P. A., Jung, M. S., Peltier, S., & Berman, M. G. (2015). Scale-free brain dynamics under physical and psychological distress: Pre-treatment effects in women diagnosed with breast cancer. *Human Brain Mapping*, *36*(3), 1077–1092. https://doi.org/10 .1002/hbm.22687, PubMed: 25388082
- Churchill, N. W., Spring, R., Grady, C., Cimprich, B., Askren, M. K., Reuter-Lorenz, P. A., ... Berman, M. G. (2016). The suppression of scale-free fMRI brain dynamics across three different sources of effort: Aging, task novelty and task difficulty. *Scientific Reports*, *6*, 30895. https://doi.org/10.1038/srep30895, PubMed: 27498696
- Churchill, N. W., Hutchison, M. G., Graham, S. J., & Schweizer, T. A. (2020). Scale-free functional brain dynamics during recovery from sport-related concussion. *Human Brain Mapping*, *41*(10), 2567–2582. https://doi.org/10.1002/hbm.24962, PubMed: 32348019
- Cocchi, L., Gollo, L. L., Zalesky, A., & Breakspear, M. (2017). Criticality in the brain: A synthesis of neurobiology, models and cognition. *Progress in Neurobiology*, 158, 132–152. https://doi.org/10.1016/j.pneurobio.2017.07.002, PubMed: 28734836
- Craddock, R. C., James, G. A., Holtzheimer III, P. E., Hu, X. P., & Mayberg, H. S. (2012). A whole brain fMRI atlas generated via spatially constrained spectral clustering. *Human Brain Mapping*, *33*(8), 1914–928. https://doi.org/10.1002/hbm.21333, PubMed: 21769991
- de Arcangelis, L., & Herrmann, H. J. (2010). Learning as a phenomenon occurring in a critical state. *Proceedings of the National Academy of Sciences, 107*(9), 3977–3981. https://doi.org/10 .1073/pnas.0912289107, PubMed: 20160107
- de Arcangelis, L., Perrone-Capano, C., & Herrmann, H. J. (2006). Self-organized criticality model for brain plasticity. *Physical Review Letters*, *96*(2), 028107. https://doi.org/10.1103 /PhysRevLett.96.028107, PubMed: 16486652
- Duff, K., Callister, C., Dennett, K., & Tometich, D. (2012). Practice effects: A unique cognitive variable. *The Clinical Neuropsychologist, 26*(7), 1117–1127. https://doi.org/10.1080/13854046.2012 .722685, PubMed: 23020261

- Duff, K., Beglinger, L. J., Moser, D. J., Paulsen, J. S., Schultz, S. K., & Arndt, S. (2010). Predicting cognitive change in older adults: The relative contribution of practice effects. *Archives of Clinical Neuropsychology*, *25*(2), 81–88. https://doi.org/10.1093/arclin/acp105, PubMed: 20064816
- Esteban, O., Birman, D., Schaer, M., Koyejo, O. O., Poldrack, R. A., & Gorgolewski, K. J. (2017). MRIQC: Advancing the automatic prediction of image quality in MRI from unseen sites. *PLoS One*, *12*(9), e0184661. https://doi.org/10.1371/journal.pone .0184661, PubMed: 28945803
- Esteban, O., Markiewicz, C. J., Blair, R. W., Moodie, C. A., Isik, A. I., Erramuzpe, A., ... Gorgolewski, K. J. (2019). fMRIPrep: A robust preprocessing pipeline for functional MRI. *Nature Methods*, *16*(1), 111–116. https://doi.org/10.1038/s41592-018 -0235-4, PubMed: 30532080
- Fagerholm, E. D., Lorenz, R., Scott, G., Dinov, M., Hellyer, P. J., Mirzaei, N., ... Leech, R. (2015). Cascades and cognitive state: Focused attention incurs subcritical dynamics. *Journal of Neuroscience*, 35(11), 4626–4634. https://doi.org/10.1523 /JNEUROSCI.3694-14.2015, PubMed: 25788679
- Farmer, S. (2015). Comment on "Broadband criticality of human brain network synchronization" by Kitzbichler MG, Smith ML, Christensen SR, Bullmore E (2009) PLoS Comput Biol 5: e1000314. PLoS Computational Biology, 11(5), e1004174. https://doi.org/10.1371/journal.pcbi.1004174, PubMed: 25950844
- Fiszdon, J. M., McClough, J. F., Silverstein, S. M., Bell, M. D., Jaramillo, J. R., & Smith, T. E. (2006). Learning potential as a predictor of readiness for psychosocial rehabilitation in schizophrenia. *Psychiatry Research*, *143*(2–3), 159–166. https://doi .org/10.1016/j.psychres.2005.09.012, PubMed: 16860881
- Fraiman, D., Balenzuela, P., Foss, J., & Chialvo, D. R. (2009). Isinglike dynamics in large-scale functional brain networks. *Physical Review E*, *79*(6), 061922. https://doi.org/10.1103/PhysRevE.79 .061922, PubMed: 19658539
- Frette, V., Christensen, K., Malthe-Sørenssen, A., Feder, J., Jøssang, T., & Meakin, P. (1996). Avalanche dynamics in a pile of rice. *Nature*, 379(6560), 49–52. https://doi.org/10.1038/379049a0
- Gautam, S. H., Hoang, T. T., McClanahan, K., Grady, S. K., & Shew, W. L. (2015). Maximizing sensory dynamic range by tuning the cortical state to criticality. *PLoS Computational Biology*, *11*(12), e1004576. https://doi.org/10.1371/journal.pcbi.1004576, PubMed: 26623645
- Gisiger, T. (2001). Scale invariance in biology: Coincidence or footprint of a universal mechanism? *Biological Reviews*, *76*(2), 161–209. https://doi.org/10.1017/S1464793101005607, PubMed: 11396846
- Glasser, M. F., Sotiropoulos, S. N., Wilson, J. A., Coalson, T. S., Fischl, B., Andersson, J. L., ... WU-Minn HCP Consortium. (2013). The minimal preprocessing pipelines for the Human Connectome Project. *NeuroImage*, *80*, 105–124. https://doi .org/10.1016/j.neuroimage.2013.04.127, PubMed: 23668970
- Goldberger, A. L., Amaral, L. A. N., Hausdorff, J. M., Ivanov, P. C., Peng, C.-K., & Stanley, H. E. (2002). Fractal dynamics in physiology: Alterations with disease and aging. *Proceedings of the National Academy of Sciences*, *99*(Suppl. 1), 2466–2472. https://doi.org/10.1073/pnas.012579499, PubMed: 11875196

- Gollo, L. L. (2017). Coexistence of critical sensitivity and subcritical specificity can yield optimal population coding. *Journal of The Royal Society Interface, 14*(134), 20170207. https://doi.org/10.1098/rsif.2017.0207, PubMed: 28954848
- Gorgolewski, K., Burns, C. D., Madison, C., Clark, D., Halchenko, Y. O., Waskom, M. L., & Ghosh, S. S. (2011). Nipype: A flexible, lightweight and extensible neuroimaging data processing framework in Python. *Frontiers in Neuroinformatics*, *5*, 13. https://doi .org/10.3389/fninf.2011.00013, PubMed: 21897815
- Hahn, G., Ponce-Alvarez, A., Monier, C., Benvenuti, G., Kumar, A., Chavane, F., ... Frégnac, Y. (2017). Spontaneous cortical activity is transiently poised close to criticality. *PLOS Computational Biology*, *13*(5), e1005543. https://doi.org/10.1371/journal.pcbi .1005543, PubMed: 28542191
- Hardstone, R., Poil, S.-S., Schiavone, G., Jansen, R., Nikulin, V. V., Mansvelder, H. D., & Linkenkaer-Hansen, K. (2012). Detrended fluctuation analysis: A scale-free view on neuronal oscillations. *Frontiers in Physiology*, *3*, 450. https://doi.org/10.3389/fphys .2012.00450, PubMed: 23226132
- He, B. J. (2011). Scale-free properties of the functional magnetic resonance imaging signal during rest and task. *Journal of Neuroscience*, *31*(39), 13786–13795. https://doi.org/10.1523/JNEUROSCI.2111-11.2011, PubMed: 21957241
- He, B. J. (2014). Scale-free brain activity: Past, present, and future. *Trends in Cognitive Sciences*, *18*(9), 480–487. https://doi.org/10.1016/j.tics.2014.04.003, PubMed: 24788139
- Ide, J. S., Hu, S., Zhang, S., Mujica-Parodi, L. R., & Chiang-shan, R. L. (2016). Power spectrum scale invariance as a neural marker of cocaine misuse and altered cognitive control. *NeuroImage: Clinical*, *11*, 349–356. https://doi.org/10.1016/j.nicl.2016.03 .004, PubMed: 27294029
- Ikkai, A., & Curtis, C. E. (2011). Common neural mechanisms supporting spatial working memory, attention and motor intention. *Neuropsychologia*, *49*(6), 1428–1434. https://doi.org/10.1016/j .neuropsychologia.2010.12.020, PubMed: 21182852
- Jaeggi, S. M., Buschkuehl, M., Jonides, J., & Perrig, W. J. (2008). Improving fluid intelligence with training on working memory. *Proceedings of the National Academy of Sciences*, *105*(19), 6829–6833. https://doi.org/10.1073/pnas.0801268105, PubMed: 18443283
- Jaffard, S., Lashermes, B., & Abry, P. (2006). Wavelet leaders in multifractal analysis. In T. Qian, M. I. Vai, & Y. Xu (Eds.), *Wavelet analysis and applications* (pp. 201–246). Springer. https://doi .org/10.1007/978-3-7643-7778-6\_17
- Jenkinson, M., Beckmann, C. F., Behrens, T. E. J., Woolrich, M. W., & Smith, S. M. (2012). FSL. *NeuroImage*, 62(2), 782–790. https://doi.org/10.1016/j.neuroimage.2011.09.015, PubMed: 21979382
- Kardan, O., Adam, K. C. S., Mance, I., Churchill, N. W., Vogel, E. K., & Berman, M. G. (2020). Distinguishing cognitive effort and working memory load using scale-invariance and alpha suppression in EEG. *NeuroImage*, 211, 116622. https://doi.org/10 .1016/j.neuroimage.2020.116622, PubMed: 32068164
- Kardan, O., Reuter-Lorenz, P. A., Peltier, S., Churchill, N. W., Misic, B., Askren, M. K., ... Berman, M. G. (2019). Brain connectivity tracks effects of chemotherapy separately from behavioral measures. *NeuroImage: Clinical*, 21, 101654. https://doi.org/10.1016 /j.nicl.2019.101654, PubMed: 30642760

- Kardan, O., Stier, A. J., Cardenas-Iniguez, C., Schertz, K. E., Pruin, J. C., Deng, Y., ... Rosenberg, M. D. (2022). Differences in the functional brain architecture of sustained attention and working memory in youth and adults. *PLoS Biology*, *20*(12), e3001938. https://doi.org/10.1371/journal.pbio.3001938, PubMed: 36542658
- Kiebel, S. J., Daunizeau, J., & Friston K. J. (2008). A hierarchy of time-scales and the brain. *PLoS Computational Biology*, 4(11), e1000209. https://doi.org/10.1371/journal.pcbi.1000209, PubMed: 19008936
- Kinouchi, O., & Copelli, M. (2006). Optimal dynamical range of excitable networks at criticality. *Nature Physics, 2*(5), 348–351. https://doi.org/10.1038/nphys289
- Kitzbichler, M. G., Smith, M. L., Christensen, S. R., & Bullmore, E. (2009). Broadband criticality of human brain network synchronization. *PLoS Computational Biology*, 5(3), e1000314. https://doi .org/10.1371/journal.pcbi.1000314, PubMed: 19300473
- Kringelbach, M. L., McIntosh, A. R., Ritter, P., Jirsa, V. K., & Deco, G. (2015). The rediscovery of slowness: Exploring the timing of cognition. *Trends in Cognitive Sciences*, 19(10), 616–628. https:// doi.org/10.1016/j.tics.2015.07.011, PubMed: 26412099
- Krishnan, A., Williams, L. J., McIntosh, A. R., & Abdi, H. (2011). Partial least squares (PLS) methods for neuroimaging: A tutorial and review. *NeuroImage*, *56*(2), 455–475. https://doi.org/10 .1016/j.neuroimage.2010.07.034, PubMed: 20656037
- Layden, E. A. (2018). *N-Back for Matlab*. Retrieved from https://doi .org/10.12751/g-node.f87128.
- Long, Z., Jing, B., Guo, R., Li, B., Cui, F., Wang, T., & Chen, H. (2018). A brainnetome atlas based mild cognitive impairment identification using hurst exponent. *Frontiers in Aging Neuroscience*, 10, 103. https://doi.org/10.3389/fnagi.2018.00103, PubMed: 29692721
- Marinazzo, D., Pellicoro, M., Wu, G., Angelini, L., Cortés, J. M., & Stramaglia, S. (2014). Information transfer and criticality in the Ising model on the human connectome. *PLoS One*, *9*(4), e93616. https://doi.org/10.1371/journal.pone.0093616, PubMed: 24705627
- McCaffrey, R. J., Duff, K., & Westervelt, H. J. (Eds.). (2013). Practitioner's guide to evaluating change with neuropsychological assessment instruments. Springer Science & Business Media. https://doi.org/10.1007/978-1-4615-4233-9
- McIntosh, A. R., & Lobaugh, N. J. (2004). Partial least squares analysis of neuroimaging data: Applications and advances. *Neuro-Image, 23*, S250–S263. https://doi.org/10.1016/j.neuroimage .2004.07.020, PubMed: 15501095
- Meisel, C., Bailey, K., Achermann, P., & Plenz, D. (2017a). Decline of long-range temporal correlations in the human brain during sustained wakefulness. *Scientific Reports*, *7*(1), 11825. https:// doi.org/10.1038/s41598-017-12140-w, PubMed: 28928479
- Meisel, C., Klaus, A., Vyazovskiy, V. V., & Plenz, D. (2017b). The interplay between long-and short-range temporal correlations shapes cortex dynamics across vigilance states. *Journal of Neuroscience*, *37*(42), 10114–10124. https://doi.org/10.1523 /JNEUROSCI.0448-17.2017, PubMed: 28947577
- Muñoz, M. A. (2018). Colloquium: Criticality and dynamical scaling in living systems. *Reviews of Modern Physics, 90*(3), 031001. https://doi.org/10.1103/RevModPhys.90.031001
- Neubauer, A. C., & Fink, A. (2009a). Intelligence and neural efficiency. *Neuroscience & Biobehavioral Reviews*, 33(7),

1004–1023. https://doi.org/10.1016/j.neubiorev.2009.04.001, PubMed: 19580915

- Neubauer, A. C., & Fink, A. (2009b). Intelligence and neural efficiency: Measures of brain activation versus measures of functional connectivity in the brain. *Intelligence*, *37*(2), 223–229. https://doi.org/10.1016/j.intell.2008.10.008
- O'Byrne, J., & Jerbi, K. (2022). How critical is brain criticality? *Trends in Neurosciences, 45,* 820–837. https://doi.org/10.1016/j .tins.2022.08.007, PubMed: 36096888
- Ouyang, G., Hildebrandt, A., Schmitz, F., & Herrmann, C. S. (2020). Decomposing alpha and 1/f brain activities reveals their differential associations with cognitive processing speed. *Neuro-Image, 205,* 116304. https://doi.org/10.1016/j.neuroimage.2019.116304, PubMed: 31654760
- Parkes, L., Fulcher, B., Yücel, M., & Fornito, A. (2018). An evaluation of the efficacy, reliability, and sensitivity of motion correction strategies for resting-state functional MRI. *NeuroImage*, 171, 415–436. https://doi.org/10.1016/j.neuroimage.2017.12 .073, PubMed: 29278773
- Peng, C. K., Havlin, S., Hausdorff, J. M., Mietus, J. E., Stanley, H. E., & Goldberger, A. L. (1995). Fractal mechanisms and heart rate dynamics: Long-range correlations and their breakdown with disease. *Journal of Electrocardiology*, 28, 59–65. https://doi.org/10 .1016/S0022-0736(95)80017-4, PubMed: 8656130
- Power, J. D., Barnes, K. A., Snyder, A. Z., Schlaggar, B. L., & Petersen, S. E. (2012). Spurious but systematic correlations in functional connectivity MRI networks arise from subject motion. *NeuroImage*, 59(3), 2142–2154. https://doi.org/10.1016/j.neuroimage.2011.10 .018, PubMed: 22019881
- Power, J. D., Mitra, A., Laumann, T. O., Snyder, A. Z., Schlaggar, B. L., & Petersen, S. E. (2014). Methods to detect, characterize, and remove motion artifact in resting state fMRI. *NeuroImage*, *84*, 320–341. https://doi.org/10.1016/j.neuroimage.2013.08 .048, PubMed: 23994314
- Proekt, A., Banavar, J. R., Maritan, A., & Pfaff, D. W. (2012). Scale invariance in the dynamics of spontaneous behavior. *Proceedings* of the National Academy of Sciences, 109(26), 10564–10569. https://doi.org/10.1073/pnas.1206894109, PubMed: 22679281
- Rapport, L. J., Brines, D. B., Theisen, M. E., & Axelrod, B. N. (1997). Full scale IQ as mediator of practice effects: The rich get richer. *The Clinical Neuropsychologist*, *11*(4), 375–380. https://doi.org /10.1080/13854049708400466
- Scott, G., Fagerholm, E. D., Mutoh, H., Leech, R., Sharp, D. J., Shew, W. L., & Knöpfel, T. (2014). Voltage imaging of waking mouse cortex reveals emergence of critical neuronal dynamics. *Journal of Neuroscience*, 34(50), 16611–16620. https://doi.org /10.1523/JNEUROSCI.3474-14.2014, PubMed: 25505314
- Sergi, M. J., Kern, R. S., Mintz, J., & Green, M. F. (2005). Learning potential and the prediction of work skill acquisition in schizo-phrenia. *Schizophrenia Bulletin*, *31*(1), 67–72. https://doi.org/10.1093/schbul/sbi007, PubMed: 15888426
- Shen, X., Tokoglu, F., Papademetris, X., & Constable, R. T. (2013). Groupwise whole-brain parcellation from resting-state fMRI data for network node identification. *NeuroImage*, *82*, 403–415. https://doi.org/10.1016/j.neuroimage.2013.05.081, PubMed: 23747961
- Shew, W. L., & Plenz, D. (2013). The functional benefits of criticality in the cortex. *The Neuroscientist*, *19*(1), 88–100.

https://doi.org/10.1177/1073858412445487, PubMed: 22627091

- Shriki, O., Alstott, J., Carver, F., Holroyd, T., Henson, R. N. A., Smith, M. L., ... Plenz, D. (2013). Neuronal avalanches in the resting MEG of the human brain. *Journal of Neuroscience*, 33(16), 7079–7090. https://doi.org/10.1523/JNEUROSCI.4286 -12.2013, PubMed: 23595765
- Shriki, O., & Yellin, D. (2016). Optimal information representation and criticality in an adaptive sensory recurrent neuronal network. *PLoS Computational Biology*, *12*(2), e1004698. https://doi.org/10.1371/journal.pcbi.1004698, PubMed: 26882372
- Sokunbi, M. O. (2018). *Children with ADHD exhibit lower fMRI* spectral exponent than their typically developing counterparts [Conference session]. Organisation for Human Brain Mapping (OHBM), Singapore.
- Stanislaw, H., & Todorov, N. (1999). Calculation of signal detection theory measures. *Behavior Research Methods, Instruments, & Computers, 31*(1), 137–149. https://doi.org/10.3758 /BF03207704, PubMed: 10495845
- Stier, A. J., Cardenas-Iniguez, C., Kardan, O., Moore, T. M., Meyer, F. A. C., Rosenberg, M. D., ... Berman, M. G. (2023). A pattern of cognitive resource disruptions in childhood psychopathology. *Network Neuroscience*, 7(3), 1153–1180. https://doi.org/10 .1162/netn\_a\_00322
- Suckling, J., Wink, A. M., Bernard, F. A., Barnes, A., & Bullmore, E. (2008). Endogenous multifractal brain dynamics are modulated by age, cholinergic blockade and cognitive performance. *Journal of Neuroscience Methods*, *174*(2), 292–300. https://doi.org/10.1016/j.jneumeth.2008.06.037, PubMed: 18703089
- Tanaka, T., Kaneko, T., & Aoyagi, T. (2008). Recurrent infomax generates cell assemblies, neuronal avalanches, and simple cell-like selectivity. *Neural Computation*, 21(4), 1038–1067. https://doi.org/10.1162/neco.2008.03-08-727, PubMed: 18928369
- Tian, Y., Tan, Z., Hou, H., Li, G., Cheng, A., Qiu, Y., ... Sun, P. (2022). Theoretical foundations of studying criticality in the brain. *Network Neuroscience*, *6*(4), 1148–1185. https://doi.org /10.1162/netn\_a\_00269
- Vohryzek, J., Cabral, J., Vuust, P., Deco, G., & Kringelbach, M. L. (2022). Understanding brain states across spacetime informed by whole-brain modelling. *Philosophical Transactions of the Royal Society A*, *380*(2227), 20210247. https://doi.org/10.1098/rsta .2021.0247, PubMed: 35599554
- Watzke, S., Brieger, P., Kuss, O., Schoettke, H., & Wiedl, K. H. (2008). A longitudinal study of learning potential and rehabilitation outcome in schizophrenia. *Psychiatric Services*, 59(3), 248–255. https://doi.org/10.1176/ps.2008.59.3.248, PubMed: 18308904
- Wei, M., Qin, J., Yan, R., Li, H., Yao, Z., & Lu, Q. (2013). Identifying major depressive disorder using Hurst exponent of resting-state brain networks. *Psychiatry Research: Neuroimaging, 214*(3), 306–312. https://doi.org/10.1016/j.pscychresns.2013.09.008, PubMed: 24113289
- Wendt, H., Abry, P., & Jaffard, S. (2007). Bootstrap for empirical multifractal analysis. *IEEE Signal Processing Magazine*, 24(4), 38–48. https://doi.org/10.1109/MSP.2007.4286563
- Werner, G. (2010). Fractals in the nervous system: Conceptual implications for theoretical neuroscience. *Frontiers in Physiology*,

1, 15. https://doi.org/10.3389/fphys.2010.00015, PubMed: 21423358

- Yu, S., Ribeiro, T. L., Meisel, C., Chou, S., Mitz, A., Saunders, R., & Plenz, D. (2017). Maintained avalanche dynamics during task-induced changes of neuronal activity in nonhuman primates. *eLife*, *6*, e27119. https://doi.org/10.7554/eLife.27119, PubMed: 29115213
- Zhuang, C., Meidenbauer, K. L., Kardan, O., Stier, A. J., Choe, K. W., Cardenas-Iniguez, C., ... Berman, M. G. (2022). Scale invariance in fNIRS as a measurement of cognitive load. *Cortex*, *154*, 62–76. https://doi.org/10.1016/j.cortex.2022.05.009, PubMed: 35753183
- Zimmern, V. (2020). Why brain criticality is clinically relevant: A scoping review. *Frontiers in Neural Circuits, 14,* 54. https://doi .org/10.3389/fncir.2020.00054, PubMed: 32982698