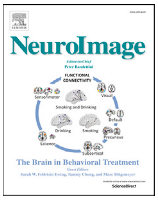
NeuroImage 172 (2018) 107–117

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/neuroimage



Predicting future learning from baseline network architecture

Marcelo G. Mattar[a,b,c,1], Nicholas F. Wymbs[f], Andrew S. Bock[e], Geoffrey K. Aguirre[e], Scott T. Grafton[g], Danielle S. Bassett[b,d,e,*]

[a] Department of Psychology, University of Pennsylvania, Philadelphia, PA 19104, USA
[b] Department of Bioengineering, University of Pennsylvania, Philadelphia, PA 19104, USA
[c] Princeton Neuroscience Institute, Princeton University, Princeton, NJ 08544, USA
[d] Department of Electrical & Systems Engineering, University of Pennsylvania, Philadelphia, PA 19104, USA
[e] Department of Neurology, University of Pennsylvania, Philadelphia, PA 19104, USA
[f] Human Brain Physiology and Stimulation Laboratory, Department of Physical Medicine and Rehabilitation, Johns Hopkins Medical Institution, Baltimore, MD, USA
[g] Department of Psychological and Brain Sciences and UCSB Brain Imaging Center, University of California, Santa Barbara, Santa Barbara, CA, USA

ARTICLE INFO

Keywords:
fMRI
Functional connectivity
Network science
Brain networks
Human learning
Motor learning

ABSTRACT

Human behavior and cognition result from a complex pattern of interactions between brain regions. The flexible reconfiguration of these patterns enables behavioral adaptation, such as the acquisition of a new motor skill. Yet, the degree to which these reconfigurations depend on the brain's baseline sensorimotor integration is far from understood. Here, we asked whether spontaneous fluctuations in sensorimotor networks at baseline were predictive of individual differences in future learning. We analyzed functional MRI data from 19 participants prior to six weeks of training on a new motor skill. We found that visual-motor connectivity was inversely related to learning rate: sensorimotor autonomy at baseline corresponded to faster learning in the future. Using three additional scans, we found that visual-motor connectivity at baseline is a relatively stable individual trait. These results suggest that individual differences in motor skill learning can be predicted from sensorimotor autonomy at baseline prior to task execution.

Introduction

Adaptive biological systems display a common architectural feature that facilitates evolvability (Kirschner and Gerhart, 1998; Kashtan and Alon, 2005; Félix and Wagner, 2008). That feature is modularity, or near-decomposability (Simon, 1965), in which the system is composed of small subsystems (or modules) that each perform near-unique functions. This compartmentalization reduces the constraints on any single module, enabling it to adapt to evolving external demands relatively independently (Kashtan and Alon, 2005; Wagner and Altenberg, 1996; Schlosser and Wagner, 2004). These principles relating modularity to adaptivity are evident across the animal kingdom, offering insights into phenomena as diverse as the developmental program of beak morphology in Darwin's finches (Mallarino et al., 2011) and the heterochrony of the skeletal components of the mammalian skull (Koyabu et al., 2014).

While an intuitive concept in organismal evolution where genetic programs drive dynamics over long time scales, it is less clear how modularity might confer functional adaptability in neural systems whose computations are inherently transient and fleeting. To gain conceptual clarity, we consider synchronization: a foundational neural computation that facilitates communication across distributed neural units (Fries, 2005; Voytek et al., 2015). Evidence from the field of statistical physics demonstrates that synchronization of a dynamical system is directly dependent on the heterogeneity of the associations between units (Gomez-Gardenes et al., 2007). Specifically, in systems where units with oscillatory dynamics are coupled in local modules, each module can synchronize separately (Arenas et al., 2006), offering the potential for unique functionality and independent adaptability. These theoretical observations become intuitive when we consider *graphs*: visual depictions of nodes representing oscillators, and edges representing coupling between oscillators (Fig. 1a). Modules that are densely interconnected will tend to become synchronized with one another, and each module will therefore be unable to adapt its dynamics separately from the other module (Arenas et al., 2006). This highly constrained state decreases the potential for adaptability to incoming stimuli in a changing environment. Conversely, modules that are sparsely interconnected with

---

* Corresponding author. Department of Bioengineering, University of Pennsylvania, Philadelphia, PA 19104, USA.
E-mail address: dsb@seas.upenn.edu (D.S. Bassett).

[1] Present address: Princeton Neuroscience Institute, Princeton University, Princeton, NJ 08540, USA.

https://doi.org/10.1016/j.neuroimage.2018.01.037
Received 30 November 2017; Received in revised form 9 January 2018; Accepted 15 January 2018

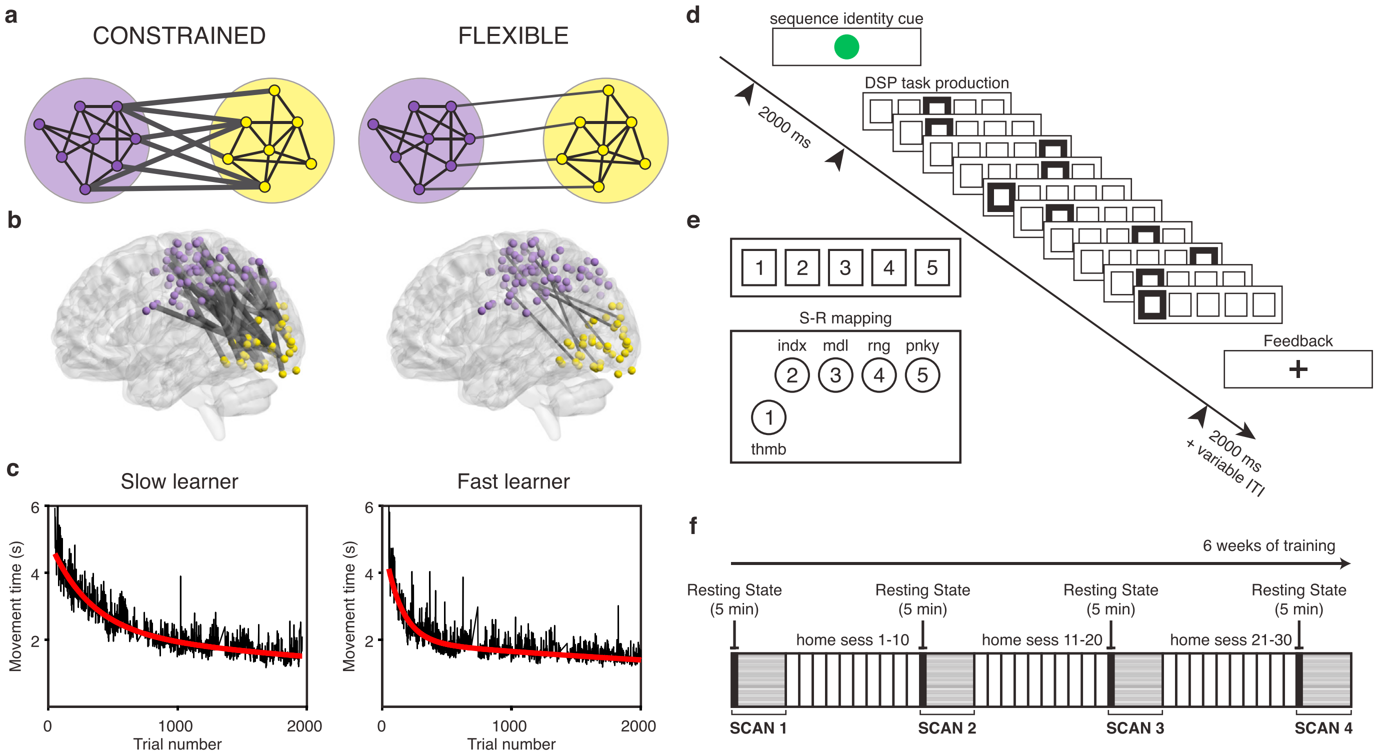


Fig. 1. Network dynamics constrain adaptive learning behavior. *(a)* The degree of connectivity between two modules can impose important constraints on the types of dynamics that are possible. A lower degree of statistical dependence between the activity profiles of two modules can allow for greater flexibility in module dynamics. *(b)* Learning a new motor skill — a sequence of finger movements — induces a progressive change in the connectivity between visual and somato-motor cortices in humans (Bassett et al., 2015). We hypothesize that individuals who display a greater functional separation, or greater modularity, between motor and visual modules at rest are poised for enhanced adaptability, and therefore will learn faster over 6 weeks of practice than individuals who display less functional separation between these modules. *(c)* Time in seconds required to correctly perform each sequence of finger movements (here referred to as *movement time*) for two example human subjects over 6 weeks of training. We observe an exponential decay in the trial-by-trial movement times for all participants (black lines), indicating that learning is occurring. The exponential drop-off parameter of a two-term exponential fit (red line) quantifies how rapidly each participant learned. Left and right panels illustrate the fits for an example slow and fast learner, respectively. *(d)* On each trial, the initial stimulus indicated which sequence should be performed. Each correct key press led to the next stimulus cue until the ten-element sequence was correctly executed. At any point, if an incorrect key was hit, a participant would receive an error signal (not shown in the figure), and the sequence would pause until the correct response was received. *(e)* Stimulus-response mapping between a conventional keyboard or an MRI-compatible button box (lower left) and a participant's right hand. *(f)* Training occurred over the course of 30 or more behavioral training sessions spanning approximately 42 days. Participants were scanned on the first day of the experiment and on three other occasions spaced approximately 1.5–2 weeks apart. Each scan session began with a 5 min resting state scan.

one another will maintain the potential for adaptive, near-independent dynamics.

Given these theoretical observations in oscillator networks, we hypothesize that human brains display a modular architecture for the explicit purpose of facilitating behavioral adaptability (Meunier et al., 2010; Bullmore et al., 2009). Such a hypothesis is bolstered by evidence that neuronal cell distributions evolve differently in regions of the brain that code for simpler reflexive *versus* more complex adaptive functions (Lewitus et al., 2012). The hypothesis also has implications for individual differences in cognitive ability across humans. Specifically, we expect that individuals that display greater modularity, or sparser connectivity, between task-specific modules should also display more behavioral adaptability in the face of novel task demands (Bassett et al., 2011, 2013, 2015) (Fig. 1b). We expect that modularity should be particularly important between low-level modules that must evolve independently; connections involving higher-level control areas could have a different relationship due to the importance of these connections in the acquisition of new skills (Cole et al., 2013).

To test these hypotheses, we studied a cohort of healthy adult human subjects who learned a new motor skill from visual cues over the course of 6 weeks (Fig. 1c). During this timeframe, recorded fMRI activity during task execution shows that learning induces a growing autonomy between motor and visual systems (Bassett et al., 2015). Here, we focused on functional connectivity *at rest* acquired from the same cohort, prior to the onset of learning. We hypothesized that individuals who display a greater functional separation, or greater modularity, between motor and visual modules *at rest* are poised for enhanced adaptability in this task, and therefore should learn faster over the 6 weeks of practice than individuals who display less functional separation between these modules. Further, we ask whether this baseline segregation between modules is a *trait* of an individual, consistently expressed over multiple scanning sessions, or a *state* of an individual, and therefore potentially responsive to external manipulation or internal self-regulation. The answers to these questions have direct implications for predicting and manipulating a human's ability to adapt its behavior — or learn — in the future.

The experimental protocol comprised of 6 weeks of training on 6 distinct motor sequences. Following a brief explanation of the task instructions, an initial MRI scan session was held during which blood-oxygen-level-dependent (BOLD) signals were acquired from each participant. The session began with a resting state scan lasting 5 min where participants were instructed to remain awake and with eyes open without fixation. During the remainder of the first scan session (baseline training), participants practiced each of 6 distinct motor sequences in a discrete sequence production (DSP) task for 50 trials each, or approximately 1.5 hr. Participants were then instructed to continue practicing the motor sequences at home using a training module that was installed by the experimenter (N.F.W.) on their personal laptops. Participants completed a minimum of 30 home training sessions, which were