

Environmental Neuroscience

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Environmental neuroscience is an emerging field devoted to the scientific study of brain-mediated, bidirectional relationships between organisms and their social and physical environments. A key feature of environmental neuroscience is the rigorous quantification of environmental features that affect the brain and subsequent behavior. In addition, environmental neuroscience considers factors that vary across multiple temporal and spatial scales that interact to produce behavior (e.g., synapses, neural circuits, cognition, local social interactions, citywide social interactions, citywide physical structures). Environmental neuroscientists then measure the spatial and temporal dynamics of the interactions between different levels of analysis. For example, we demonstrate through hierarchical systems theory and mathematical modeling how interacting with urban greenspace may reduce psychopathology via improvements in neurocognitive functioning, which, in turn, may increase social interactions. This example illustrates how different levels of analysis (e.g., neurocognitive factors, the physical environment, and the social environment) may be combined to understand behavior in novel ways. In addition, we advocate for the collection of data across these scales and measuring their interactions, which will generate rich data sets that will continue to yield insights as new ways to model these complex multilevel systems are developed. We believe that examining all of these levels of analysis at different temporal and spatial scales in addition to modeling their relationships will lead to advances in understanding behavior.

Public Significance Statement


This article outlines the emerging field of environmental neuroscience that examines the bidirectional relationships between the neural processes of organisms and their interaction with their physical and social environments. Environmental neuroscience considers factors that vary across multiple temporal and spatial scales that interact to produce behavior and places a special emphasis on the rigorous quantification of the external physical environment. Collecting data across these scales and measuring their interactions will generate rich data sets that will continue to yield insights while new ways to model these complex multilevel systems are developed. Ultimately, this will lead to advances in understanding behavior.

Keywords: environmental neuroscience, network neuroscience, hierarchy theory, complex systems, environmental psychology

Neuroscientists, psychologists, geneticists, sociologists, economists, and philosophers have long worked toward

understanding the mechanisms and causes of human behavior. In the past two decades, an explosion of research has

Editor's note. Marc G. Berman received a 2019 APA Award for Distinguished Scientific Early Career Contributions to Psychology. This article was invited in relation to the award, formally bestowed at the 127th Annual Convention of the American Psychological Association, held August 8–11, 2019, Chicago, Illinois.

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This work was inspired by one of Marc G. Berman's mentors, Stephen Kaplan (1936–2018), and Marc G. Berman's paternal grandparents, Ella and Ludwig Berman, whose lives as Holocaust survivors

motivated him to study the mind; and to Marc G. Berman's maternal grandparents, Ruth E. and Merl G. Swann, who were also a great inspiration to Marc G. Berman.

This work was supported in part by a grant from the TKF Foundation to Marc G. Berman, a grant from the National Science Foundation (BCS-1632445) to Marc G. Berman, as well as an internal grant from the University of Chicago to Marc G. Berman. Andrew J. Stier and Gaby N. Akcelik contributed equally to this work and order is arbitrary.

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demonstrated that changes in the external sociophysical environment can significantly and persistently impact cognition and behavior (Berman, Kardan, Kotabe, Nusbaum, & London, 2019; Keize, Lindenberg, & Steg, 2008; Kotabe, Kardan, & Berman, 2016). At the same time, theoretical developments have provided a framework for understanding why brains are fundamentally and causally intertwined with the external environment (see Clark, 1999, for a summary, or Salge, Glackin, & Polani, 2014, for an information-theoretic perspective). These developments have implied that the social and physical environment that surrounds us is an active participant in creating variability in human and nonhuman animals' behavior. In other words, simply controlling for, or regressing out, environmental context is not sufficient to truly understand behavior. Instead, the temporal and spatial dynamics of interactions between individuals (and groups of individuals) and the environment must be considered in both the experimental design and model

building phases when studying behavior. Consequently, environmental neuroscience (Berman et al., 2019) has emerged as the scientific study of brain-mediated, bidirectional relationships between organisms and their social and physical environment.

To be effective, environmental neuroscience must consider how processes and factors that vary across multiple scales of temporal and spatial resolution (see Figure 1) interact to produce behavior. Other frameworks have attempted to do this, such as the multilevel frameworks of social neuroscience (Cacioppo & Decety, 2011) and network neuroscience (Bassett & Sporns, 2017). Here, it is important to model interactions within a level (e.g., brain network connectivity) and also between levels (e.g., the relationship between brain network connectivity and genomic function). Environmental neuroscientists measure the spatial and temporal dynamics of the interactions between levels of analysis, such as how being a carrier of

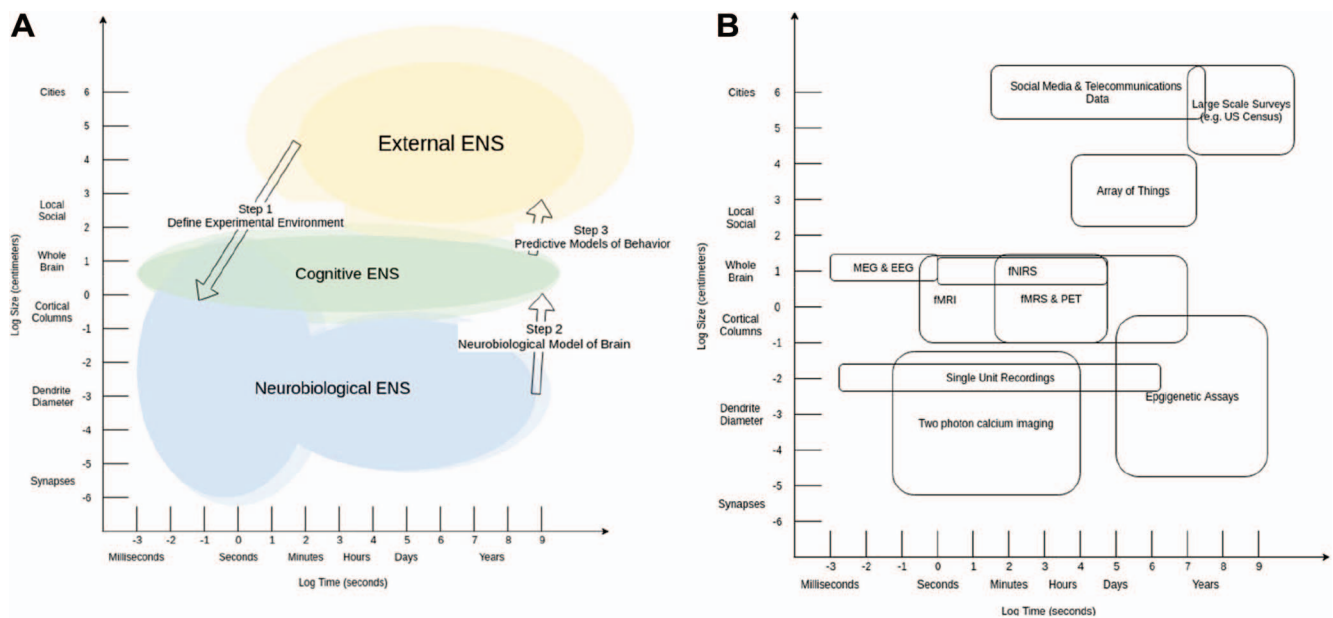


Figure 1. The spatial and temporal scales of environmental neuroscience (ENS). (A) A granular characterization of the scales of environmental neuroscience. At the smallest spatial scale, covering genomic processes and synapses to small sections of the brain (from approximately 10^{-6} cm to approximately 10^2 cm), is neurobiological ENS, which is concerned with the environment as it relates to neurobiological processes internal to an organism. At an intermediate spatial scale, covering small sections of the brain to the whole brain (from approximately 10^1 cm to approximately 10^3 cm), is cognitive ENS, which considers the environment as it relates to the cognitive processes of whole organisms. At the largest spatial scale, covering the whole brain to entire cities (from approximately 10^3 cm to approximately 10^6 cm and beyond), is external ENS, which considers spatially extended interactions between individual organisms and the physical environment as well as interactions between an individual and groups of individuals. (B) Methods that provide access to the different temporal and spatial scales of environmental neuroscience, as adapted by permission from Springer Nature Publishing, Nature Neuroscience, "Network Neuroscience," by D. S. Bassett and O. Sporns, Copyright 2017. Array of Things is a citywide sensor network in Chicago, Illinois, that has been extended to other cities across the United States and the world. fMRI = functional magnetic resonance imaging; MEG = magnetoencephalography; EEG = electroencephalography; PET = positron emission tomography; fMRS = functional magnetic resonance spectroscopy; fNIRS = functional near-infrared spectroscopy. See the online article for the color version of this figure.

certain genetic polymorphisms (Belsky et al., 2009) may affect how interactions with urban greenspace may or may not benefit an individual (Berman et al., 2019). We believe that examining all of these levels at different temporal and spatial scales will lead to advances in understanding behavior. In addition, the collection of data across these scales and measuring their interactions will generate rich data sets that will continue to yield insights as new ways to model complex multilevel systems are developed.

The goals of environmental neuroscience were first outlined in an earlier article (Berman et al., 2019) as the following: (a) to place the physical and social environment at the forefront and to link human and nonhuman animal research together by finding brain measures that could be compared across species (e.g., brain network properties, nonlinear dynamics), (b) to identify the qualitative and quantitative relationships between different levels of biological and environmental analyses, (c) to examine humans across the life span, (d) to compare complex human physical and social environments with that of other species and to potentially manipulate those nonhuman environments in ways that humans have manipulated their own environments, and (e) to attempt to use this information to design and reform the physical environment in order to improve human psychological functioning (Berman et al., 2019).

To achieve these goals, environmental neuroscientists will attempt to *causally predict behavior* in healthy and clinical populations by combining measurements of the social and physical environment with data from individual neurobiology, epigenetics, and psychology. In addition, environmental neuroscientists will attempt to *explain the qualitative and quantitative mechanisms* that mediate the relationship between neurobiology, epigenetics, psychology, and the external environment. Prediction and explanation are two distinct scientific goals; certain questions, experimental settings, and data favor one paradigm over the other (Yarkoni & Westfall, 2017). For example, explaining how neurons work (e.g., ion depolarization) is not sufficient for predicting an organism's behavior. Likewise, the prediction of an individual's behavior based on one's desires and preferences (Bachrach, Kosinski, Graepel, Kohli, & Stillwell, 2012) cannot on its own yield insight into the causal epigenetic, neurobiological, and neural network mechanisms by which an individual's motivations and preferences generate behavior. However, these goals are not mutually exclusive and are not independent: Good predictive models can pave the way for better explanation, and better explanation can improve predictive models (Yarkoni & Westfall, 2017). In short, environmental neuroscientists employ methods from sociology, psychology, neurobiology, and epigenetics to predict and explain how the properties of neurobiological systems at various spatial scales (e.g., synapses, neural circuits, cognition, local social interactions, citywide social interactions, and citywide physical struc-

tures) mediate the bidirectional relationships between organisms and their environment at time scales ranging from fractions of seconds to decades.

In order to accomplish this, environmental neuroscientists need to consider how they sample participant populations. Although there have been significant efforts in psychology to increase the ecological validity of population sampling, environmental neuroscientists need to pay particular attention to this (Henrich, Heine, & Norenzayan, 2010). Environmental neuroscientists are interested in assaying the diversity of environmental contexts in which modern humans live. Therefore, environmental neuroscientists have to sample diverse populations within industrialized urban/suburban areas that vary in many physical and sociological attributes as well as studying populations who inhabit less developed, and more "natural," areas. This requires sampling individuals from diverse populations that reside in diverse and varied physical and social environments (e.g., urban, rural, industrial, agricultural, communal, tribal). This is particularly important in the context of increasing global urbanization (Dye, 2008), which will see 2.5 billion people move into urban areas by 2050, thus altering the physical and social environment for many humans across the planet.

The Origins of Environmental Neuroscience

Environmental neuroscience has its roots in early behavioral neuroscience work, such as Donald Hebb's (1949) observation that rats reared in complete darkness show behavioral differences in visual perception compared with rats reared normally, and Blakemore and Cooper's (1970) discovery that these environmentally evoked perceptual differences are driven by experience-dependent neuronal reorganization. Blakemore and Cooper compared cats raised in visual environments consisting of horizontal or vertical stripes and found that the drastic manipulation of the cats' early visual environment produced equally drastic and consistent reorganization of their visual cortices. Later work by Greenough and colleagues (Benefiel & Greenough, 1998; West & Greenough, 1972) found that subtle differences in animals' environments, such as the presence or absence of toys, having "free play," and having access to running wheels, also induced differences in cortical structure, function, and behavioral performance. This and other early work demonstrated that, in nonhuman animals, exposure to different physical and social environments during development causally impacts neurobiology and subsequent behavior. In the 21st century, modern noninvasive neuroimaging has allowed researchers to extend these ideas beyond ontogeny and to translate them to human settings. Researchers have shown that human brains undergo functional and structural changes in response to social and physical environmental stimuli, including restored attention in natural settings (Berman, Jonides, & Kaplan, 2008), sharpening of neural rep-

resentations with cultural learning (Dehaene et al., 2010), reduced cortical thickness in children with lower socioeconomic status (Lawson, Duda, Avants, Wu, & Farah, 2013), and altered white matter tracts in children exposed to air pollution (Pujol et al., 2016).

Thus, past and current research in environmental neuroscience has typically focused on the unidirectional impact of the external environment on behavior and neurobiology (i.e., external → behavior/brain). However, the modern experience of humanity is set against the backdrop of a human-designed environment (Clark, 2016) created by constant manipulation of the external physical and social environment. Along these lines, Winston Churchill (1943) once famously said, “We shape our buildings and afterwards our buildings shape us”. Early work by Milgram (1970) recognized the existence of this bidirectional pathway in which humans create their environment and are then subsequently changed by it (i.e., behavior/brain → external environment → behavior/brain). Milgram correctly hypothesized that the sociophysical alterations associated with urbanization both benefit people in the form of infrastructural economies of scale and increased creativity (among others) but also come with negatives in the form of increased crime, pollution, and suicide rates (Bettencourt, Lobo, Helbing, Kühnert, & West, 2007; Melo, Moreira, Batista, Makse, & Andrade, 2014). These human alterations of the environment, by their nature, introduce a cacophony of new sounds, sights, and physical and social cues (e.g., street signs, advertisements, and architecture) along with new social structures not present in the early evolutionary environment in which human brains evolved (Dehaene & Cohen, 2007). Urbanization has also allowed humans to live in more densely populated areas and has humans spending more time indoors than outdoors. As such, there is a need for a science that examines (a) the extent to which these constructed sociophysical environments impact human behavior, cognition, and well-being (Dehaene & Cohen, 2007), and (b) uncovering the characteristics of human neurobiology and cognition, which lead to the creation of these constructed environments, which then feedback to affect neurobiology and cognition.

In seeking to understand how the modern physical and social environment interacts with brain and behavior, environmental neuroscience has converged on ideas that have parallels in developmental systems theory (DST; see Oyama, Griffiths, & Russell, 2001, for an introduction) and similar approaches such as neuroconstructivism (Westermann et al., 2007). In particular, DST has long supported the view of organisms being inextricably intertwined with their external environments (Griffiths & Tabery, 2013; Oyama et al., 2001) and, consequently, has long argued for the necessity of a multiscale-dynamics approach (Griffiths & Tabery, 2013), which environmental neuroscience is in agreement with. Environmental neuroscience is also in agreement with DST in examining the bidirectional rela-

tionships between environmental structures and brain function (Griffiths & Tabery, 2013) rather than a unidirectional relationship of environmental structures on brain function. Additionally, environmental neuroscience agrees with the importance of looking at the dynamics of a system, as earlier environmental exposures and experiences can affect later development (Ford & Lerner, 1992; Griffiths & Tabery, 2013). However, because DST asserts the irreducibility of organism–environment systems, it becomes difficult to develop hypotheses that can be experimentally tested (Shea, 2011). In contrast, although environmental neuroscience recognizes the need for multiscale approaches, it also recognizes the need for a concrete modeling framework for evaluating when interactions between distinct levels of analysis are important. Under such a framework, environmental neuroscientists can condense the “interactionist soup” (Shea, 2011) associated with DST and more easily develop actionable research programs.

DST rejects the validity of attempting to “partition causal responsibility . . . into additive components” (Oyama et al., 2001), whereas environmental neuroscience aims to model the nature and strength of interactions between mostly independent components and empirically quantify their interactions. This means that environmental neuroscience emphasizes testing these interactions empirically to determine independence and codependence between components. Relatedly, environmental neuroscientists must determine when modeling a phenomenon as an amalgam of interacting components is appropriate and when it is not. As such, environmental neuroscience is not limited to phenomena that require a fully interactionist point of view. So although environmental neuroscience shares and builds off of many of the ideas of DST and neuroconstructivism, there are enough differences that make the fields separable.

Environmental neuroscience also distinguishes itself from these parallel fields by the great lengths to which environmental neuroscience takes to quantify many aspects of the physical environment, including quantifying the amount of greenspace, fractalness, visual disorder, noise, particulate matter, and ambient temperature in the physical environment and how those factors, in turn, affect behavior (Berman et al., 2019). Finally, it is important to highlight that environmental neuroscience is fundamentally a neuroscience and is interested in phenomena that involve the brain and its interactions with the environment. As a consequence of this, environmental neuroscience is not interested in phenomena that can be understood without recourse to the brain. For example, a current pressing issue in the United States has to do with citizens’ views on gun control. Although incredibly important, understanding why people in different cities or states have divergent views on gun control does not require explanations at the neural or genetic level. A researcher could determine one’s views on gun control by examining one’s ethnicity, political affiliations, zip code,

employment, and so forth. All of this could be identified by surveying people with various questionnaires. Researched in this way, one's views on gun control would not fit squarely as a question for an environmental neuroscientist.

In the remainder of this article, we introduce a conceptual framework for evaluating when interactions between different levels of analysis/organization are important and demonstrate how to apply this framework to a quintessential environmental neuroscience example: the effects of urban greenspace.

Environmental Neuroscience Is a Multiscale Science

The vast spatial scales, from synapses to cities, and vast temporal scales, from milliseconds to decades to millennia, over which interactions between the sociophysical environment and our brains occur present environmental neuroscientists with a daunting phenomenological space to explore. For example, understanding the impact of urban greenspace on human behavior and well-being (Berman et al., 2008; Kardan, Gozdyra, et al., 2015) requires understanding what types of behaviors urban greenspace affects. These could include individual cognition, psychopathology, family dynamics, and neighborhood crime levels. One would also want to know the amount of exposure required for the effects to manifest—for example, individual effects may be realized after seconds of exposure (Kotabe et al., 2016; Van Hedger, Nusbaum, et al., 2019) or after years (Chetty, Hendren, & Katz, 2016; Kardan, Gozdyra, et al., 2015)—and how the effects may vary for individuals (e.g., different genetic sensitivity; Belsky et al., 2009; Berman et al., 2019). It would also be important to know how urban greenspace induces structural or functional changes in the brain (Berman et al., 2019). In general, the processes that environmental neuroscience aims to study operate across various spatial and temporal scales. However, current methods, like single-unit neural recordings, functional MRI, and graph-theoretic social network analyses, typically only offer access to isolated spatial and temporal scales. The question for environmental neuroscientists, then, is how and when to apply and develop methods that account for the interactions that take place *across* spatial and temporal scales.

One approach to answering this question is to draw on a theoretical framework from complex and hierarchical systems theory (see Jordan, Srinivasan, & van Leeuwen, 2015, and Smith & Sage, 1973, for a mathematical introduction). This framework helps environmental neuroscientists decompose brain-mediated relationships between organisms and their sociophysical environment into phenomena that can be studied semi-independently with existing methods. Additionally, hierarchy theory provides well-developed

mathematical frameworks that can explicitly guide complex systems modeling approaches (Langellier et al., 2019; Zhou, Smith, & Sharpee, 2018).

Hierarchical System Theory as Applied to Environmental Neuroscience

Hierarchical systems are natural models for environmental neuroscientists because spatial scales of biological organization are typically nested within one another. For example, in environmental neuroscience phenomena, in which the brain mediates interactions between behaviors and the external environment, the hierarchical levels include, but are not limited to, proteins (which are subcellular), neurons (which are nested within the brain), the brain (which is suborganismal), people (who are embedded in social networks), and societies (which are embedded in the world at large; see Figure 2). In order to achieve the goals of causal prediction and explanation, environmental neuroscientists must understand the mechanisms that exist at each hierarchical level and how the levels are linked to each other. The fields on which environmental neuroscience builds upon (e.g., network neuroscience) have done an excellent job investigating interactions within hierarchical levels. They have also made great progress in understanding the hierarchical (multiscale) context of many studied interactions. Environmental neuroscience innovates on these successful frameworks by explicitly considering the spatial and temporal dynamics of the interactions between hierarchical levels (e.g., epigenetic, neural network, cognitive and external environment levels). Consequently, the idea of *coupling strength* from hierarchical complex systems theory (see Pattee, 1973, for a review) provides a useful conceptual framework to aid in enumerating and linking mechanisms across hierarchical levels (different scales).

One of the key tenets of hierarchical systems theory is that it is often easier to handle several lower order subsystems that interact with each other rather than one larger system of a higher order (Smith & Sage, 1973). For example, it is likely easier to understand the behavior of smaller neural ensembles that make up larger neural networks rather than trying to understand the behavior of whole-brain networks all at once. This is not to say that neuroscientists should not attempt to examine the whole brain at once—this is what most neuroscientists do who use neuroimaging techniques; however, much can be gained from viewing the brain as a collection of smaller parts that interact with each other. Understanding the interactions of these subsystems is then critical toward understanding the system as a whole. In hierarchical systems theory, the strength of the interactions and dependencies between these subsystems is known as *coupling strength*. The coupling strength of a hierarchical system determines to what degree hierarchical levels and subsystems within and between levels depend on one an-

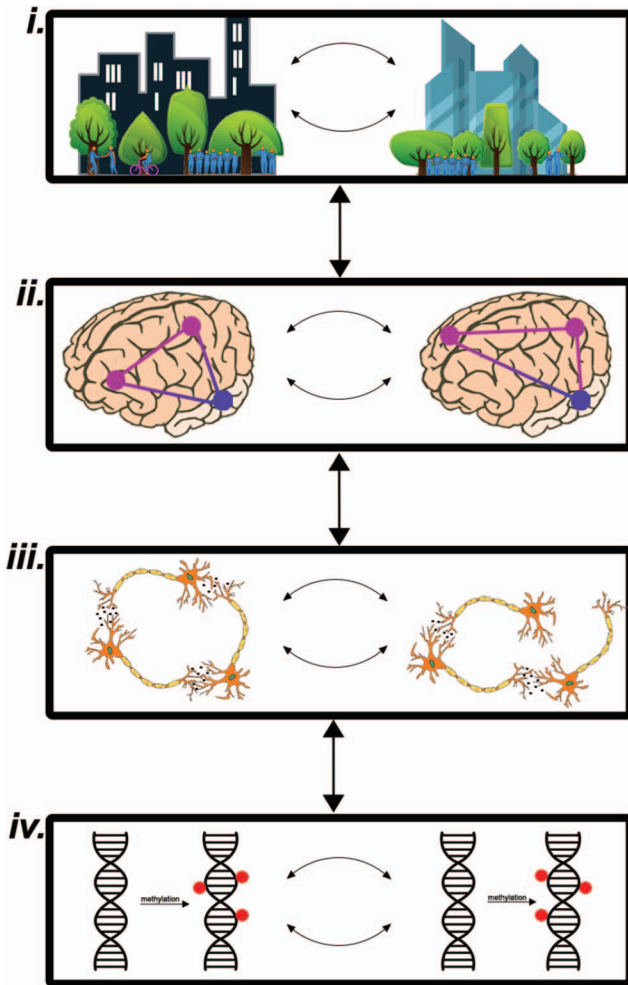


Figure 2. The hierarchical organization of environmental neuroscience phenomena. Environmental neuroscience phenomena have a nested hierarchical structure, with dynamics both between and within hierarchical levels. It is important for environmental neuroscientists to measure both the dynamics within hierarchical levels and the coupling strength between hierarchical levels. (i) Human environments can be modified to change many properties such as somatosensory properties, ecological properties, chemical properties, social institutional properties, and so forth. (ii) Global brain dynamics can reveal changes in functional connectivity and network dynamics. (iii) Neural plasticity allows networks of neurons to modify their connectivity structure. (iv) Epigenetic dynamics can change gene expression levels. See the online article for the color version of this figure.

other. If the coupling *between* levels/subsystems is weak, then each level/subsystem has only a limited impact on the dynamical repertoire of other levels. Conversely, if the coupling between levels/subsystems is strong, then each level/subsystem has a large impact on other levels. In most psychology and neuroscience contexts, when researchers do examine more than one scale of analysis, they typically default to assuming a linear relationship between scales/levels. From an environmental neuroscience perspective, one would try to fit more descriptive models to describe the

dependencies and interactions between subsystems, and once this model was fit, the coupling strength can be operationalized quantitatively. In this way, coupling strength is a quantitative generalization of what psychologists and neuroscientists typically refer to as an interaction.

To make this more concrete, let us consider an example from dyadic problem solving. In dyadic problem solving, two people are working together to try to solve a problem. In this case, it is easy to see the component subsystems (i.e., each person in the dyad) and the higher order system (i.e., the two people working together to solve the problem). In some interesting work from [Abney, Paxton, Dale, and Kello \(2015\)](#), the authors examined the coupling between each member of the dyad and related that coupling to their success in solving a problem, in this case, building the tallest possible tower out of uncooked spaghetti and marshmallows. Abney et al. measured the coupling strength between each member of the dyad by measuring the similarity in body movements between each member of the dyad or, rather, how synchronized each person's movements in the dyad were. This was done via cross-recurrence quantification analysis (CRQA; [Coco & Dale, 2014](#)), which is a nonlinear data analysis technique used to quantify the number of recurrent events in a dynamic system. Abney et al. observed that dyads whose movement patterns were more strongly coupled (i.e., had more mimicry/synchrony) performed worse at assembling the towers of spaghetti and marshmallows. In this case, and maybe somewhat counter-intuitively, the weaker coupling between the two people may have granted more flexibility in their joint problem solving and may have allowed them to adapt more easily to task constraints ([Abney et al., 2015](#)). Presumably, in other tasks, higher synchrony may be advantageous. This example illustrates how we can decompose a larger system (a dyad of two people solving a problem) into component subsystems, each person individually, and measure their coupling (in this case, movement synchrony as determined by CRQA) and how that relates to the overall system performance, that is, dyadic problem-solving success. To make the Abney et al. example more of an environmental neuroscience problem, an environmental neuroscientist may probe how changing the lighting in the environment, the amount of ambient sound, or the ambient temperature affected the coupling strength between the people and subsequent problem-solving success. In addition, an environmental neuroscientist might also measure brain activity patterns of each member of the dyad to uncover how neural network properties might relate to the coupling strength between each dyad member. In fact, researchers have begun to examine how brain network patterning relates to social network patterning ([Noonan, Mars, Sallet, Dunbar, & Fellows, 2018](#)) and to the amount of childhood exposure to individuals from multiethnic backgrounds ([Cloutier, Li, Mišić, Correll, & Berman, 2017](#)).

In the next section, we consider how the neurocognitive benefits associated with exposure to greenspace (e.g., increased working memory capacity; Berman et al., 2008) interacts with the number of per capita social interactions that an individual may have. Research has suggested that interacting with urban green space can increase social interactions (Kuo, 2003; Peters, Elands, & Buijs, 2010), and it is possible that one mechanism for this might be through improving/increasing working memory capacity (Kaplan & Berman, 2010). These working memory benefits are likely related to alterations in brain network functioning after interactions with nature, which is an active area of research in environmental neuroscience (Berman et al., 2019).

In order to quantify these relationships, we consider (a) the effects of urban greenspace on neurocognitive performance (Berman et al., 2008), (b) the geometry of the infrastructure networks in cities (e.g., roads, electrical wiring, water pipes, etc.), and (c) how people move through cities (Bettencourt, 2013). By combining these multiple levels and operationalizing their coupling strength, we demonstrate that different dose–response curves for the neurocognitive effects of greenspace on working memory result in greenspace having stronger or weaker impacts on the number of per capita social interactions that a person would have.

A Specific Environmental Neuroscience Example: The Impact of Urban Greenspace

One area of study in environmental neuroscience examines how interacting with more natural environments can be beneficial for cognition, affect, and health in both human and nonhuman species (Berman et al., 2012; Bourrier, Berman, & Enns, 2018; Bratman et al., 2019; Bratman, Hamilton, & Daily, 2012; Lambert et al., 2016; Lambert, Nelson, Jovanovic, & Cerdá, 2015; Markham & Greenough, 2004). When we refer to *natural environments*, we refer to environments that have elements of nature, such as trees, water, grass, and so forth (Hartig, Mitchell, de Vries, & Frumkin, 2014). However, not all natural environment interventions require that the stimulation be “real,” as studies have shown that the effects can be achieved via interactions with pictures of nature, videos of nature, and exposure to nature sounds (Berman et al., 2008; Bourrier et al., 2018; Gamble, Howard, & Howard, 2014; Valtchanov, Barton, & Ellard, 2010; Van Hedger, Nusbaum, et al., 2019).

We know quite a bit about the cognitive and affective benefits that are attained by humans when interacting with nature at short and long time scales. Research has shown that brief interactions with nature can increase working memory capacity (Berman et al., 2008, 2012; Berto, 2005; Bratman, Daily, Levy, & Gross, 2015; Stenfors et al., 2019), improve mood (Bratman et al., 2015; McMahan & Estes, 2015), and increase attention (Berman et al., 2008). Longer term exposures have been linked to reduced crime (Kuo &

Sullivan, 2001), increased well-being (Cimprich & Ronis, 2003; MacKerron & Mourato, 2013), increased health (Engemann et al., 2019; Kardan, Gozdyra, et al., 2015; Mitchell & Popham, 2008), and improved school outcomes (Dadvand et al., 2015).

We are, however, lacking the knowledge about why such effects manifest. There have been a number of theories that propose why interacting with nature might increase cognitive performance, such as attention restoration theory (Kaplan, 1995; Kaplan & Berman, 2010), stress reduction theory (Ulrich et al., 1991), perceptual fluency (Joye & Van den Berg, 2011), biophilia (Kellert & Wilson, 1993), and prospect-refuge theory (Appleton, 1975). Some of the above theories allude to biological mechanisms but do not examine those levels of scale head on. Understanding the biological mechanisms of these effects may lead to better predictive models for how and why environments will affect people, which could lead to improved environmental designs.

An environmental neuroscience approach to this problem might be to first start with the perceptual features that differ between natural and urban environments given that simply perceiving movies, pictures, and sounds of more natural versus more built stimulation alters cognitive performance (Berman et al., 2008; Berto, 2005; Bourrier et al., 2018; Stenfors et al., 2019; Van Hedger, Nusbaum, et al., 2019). There is now a growing literature enumerating the low-level visual and acoustic features that differentiate natural from urban/built scenes (Berman et al., 2014; Coburn et al., 2019; Kardan, Demiralp, et al., 2015; Kotabe, Kardan, & Berman, 2017; Schertz & Berman, 2019; Van Hedger, Huang, Nusbaum, & Berman, 2019), and it is possible that simply perceiving these features may have cognitive benefits based on how human brains are organized (Berman et al., 2019; Figure 3, Panels ii and iii). In fact, researchers have shown that perceiving images that have fractal stimulation similar to nature places the brain in a low-effort state, as measured with electroencephalography (EEG; Hägerhäll et al., 2015). Part of this may also be due to the structure of natural scenes and natural scene statistics (Olshausen & Field, 2000), which may then lead to lower information costs compared with the processing of urban environment stimulation (Zénon, Solopchuk, & Pezzulo, 2019). In fact, in nonhuman species, it has been found that groups of neurons in the retina encode predictive information differently for naturally occurring stimuli when compared with artificial, experimenter-constructed stimuli (Palmer, Marre, Berry, & Bialek, 2015). All of this suggests that some of the salubrious effects of interacting with nature, at short time scales, may have to do with perceiving the perceptual features of nature (Schertz & Berman, 2019; Schertz et al., 2018) that the brain may process more easily and efficiently (Berman et al., 2019).

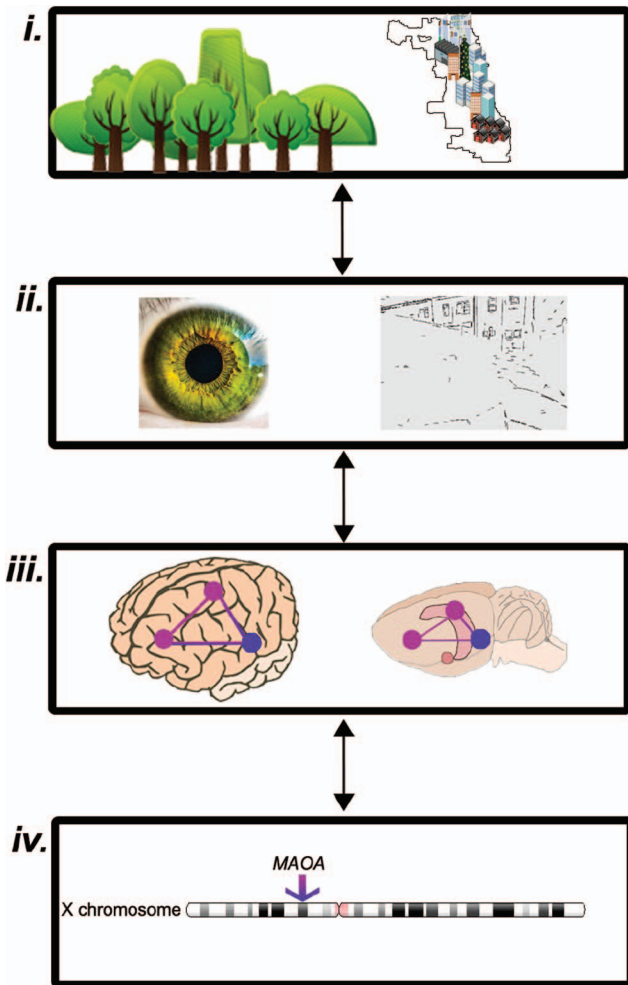


Figure 3. The hierarchical organization of urban greenspace effects. The effects of interactions with urban greenspace can be characterized by four main levels of analysis: (i) greenspace density, diversity, and proximity to different neighborhoods; (ii) perception of the low-level features of natural stimulation, such as fractalness and curved edges; (iii) neural network alterations after interacting with such stimulation that may be conserved across species; and (iv) genomic variability that may predict whether individuals are more or less influenced by urban greenspace. MAOA = monoamine oxidase A. See the online article for the color version of this figure.

At larger spatial scales and longer temporal scales, there has been evidence that neighborhood greenspace can have positive effects on city inhabitants. For example, research has shown that proximity to neighborhood greenspace is related to better physical health (Kardan, Gozdyra, et al., 2015), lower mortality (Mitchell & Popham, 2008), improved school performance (Dadvand et al., 2015), and better mental health (Engemann et al., 2019). It is possible that some of these effects are partly due to the perceptual features of nature (Schertz & Berman, 2019) but likely also due to natural environments improving air quality (Nowak, Hirabayashi, Bodine, & Greenfield, 2014), increasing the

propensity to exercise (Thompson Coon et al., 2011), increasing social cohesion (de Vries, van Dillen, Groenewegen, & Spreeuwenberg, 2013; Maas, van Dillen, Verheij, & Groenewegen, 2009), and reducing exposure to toxins (Nowak, Crane, & Stevens, 2006).

This rich set of positive effects of urban greenspace makes it possible to ask a number of multiscale questions. For example, could increase exposure to greenspace lead to better mental health outcomes by improving neurocognitive functioning, which could then increase the quality and rate of social interactions, thus leading to improved mental health? To understand these multiscale relationships in more detail, one might first try to determine the boundary conditions for how much exposure to greenspace is required to observe neurocognitive effects. A follow-up question might be to determine how these effects scale with more exposure and at what exposure levels the benefits asymptote. In effect, one would be attempting to quantify the dose–response relationship between greenspace and neurocognitive restoration (Bratman et al., 2019). This might require manipulating the physical features of the environment and exposing human and nonhuman animals to these physical features (e.g., fractalness) and measuring how perceiving these features alters brain structure and function, and how those changes relate to changes in neurocognitive performance (Berman et al., 2019; Schertz & Berman, 2019).

Once the specific time-scale dynamics of neurocognitive restoration from greenspace are known, one can begin to explore how strongly these dynamics influence social interactions. A naive multiscale approach might involve computing the correlation between greenspace coverage and the number of social interactions per capita in different neighborhoods of cities. This approach, although informative, does not address the possibility that greenspace affects social interactions in nonadditive ways.

Instead, we can look to the mathematical models of how information, people, and goods move through cities (Betencourt, 2013) and apply them here. A fundamental result from this theory is that the number of social interactions per capita, \bar{I} , obeys a scaling law with respect to the population of a city: $\bar{I} \sim a_0^{1/3} l^{4/3} C_{phys} N^{1/6}$, where N is the population, C_{phys} is a constant based on the geometry of cities' infrastructure networks, l is the typical distance traveled by an individual, and a_0 is the social interaction cross-section, which, in effect, gives the probability of a person having a social interaction per unit area. Under the hypothesis that individuals who experience more neurocognitive restoration from greenspace are more likely to interact with others in positive ways (Kaplan & Berman, 2010; Kuo & Sullivan, 2001), we can replace a_0 with a new quantity a_g that depends on greenspace coverage. We can further make the assumption that a_g is driven by the dose–response curve between greenspace (g) and cognitive restoration (i.e., $a_g \sim g$).

Then, depending on the shape of the dose–response curve, we will obtain different coupling strengths between greenspace coverage and the number of social interactions per person (see Figure 4).

If the dose–response curve is linear and positive, the marginal effect of greenspace on social interactions decreases as more greenspace is added, with $\bar{T} \sim g^{1/3}$. In this case, the shape of the dose–response curve and the structure of the mathematical model combine to produce strong coupling between the cognitive level of analysis and the social-network level of analysis (see Figure 4). However, if the dose–response curve is sigmoidal, the marginal effect of greenspace on the number of social interactions decreases much faster than in the linear case, $\bar{T} \sim (1/(1 + e^{-g}))^{1/3}$. This effectively limits the range over which greenspace influences social interactions via the neurocognitive restoration mechanism. In this case, there is a limited range in which the neurocognitive and social network levels of analysis are strongly coupled. Outside of this range, there is loose or weak coupling between these levels of analysis (see Figure 4). One way to operationalize this coupling strength is by measuring the dynamic range over which effects manifest. Here, we can define the dynamic range as $\Delta = 10 * \log_{10}(g_{90}/g_{10})$, where, for example, g_{10} is the greenspace exposure level when \bar{T} reaches 10% of its total response, g_{90} is the greenspace exposure level when \bar{T} reaches 90% of its total response and the dynamic range Δ has units

of decibels (Gautam, Hoang, McClanahan, Grady, & Shew, 2015). With this definition, the linear dose–response curve yields a dynamic range of 28 db, whereas the sigmoidal dose–response curve yields a dynamic range of 3.8 db. This means that in the linear case, the neurocognitive and social levels of analysis are more tightly coupled, whereas in the sigmoidal case, they are more loosely coupled because the effects of neurocognitive restoration via greenspace exposure on social interactions happens over a smaller range of greenspace exposure.

How might this model be extended for predicting mental health? To examine this, one would need to add another layer in the hierarchical system that connected increased social interactions from urban greenspace (via neurocognitive restoration) to mental health. In the linear case in which increased greenspace led to linear increases in cognitive performance, the range over which greenspace interacts with social interactions is extremely large. For example, the greenspace range may go from “0,” which could be represented by an industrial park, to “1,” representing a forest. The number of variables that differs between these two extreme environments is immense. For example, in comparing these two extremes, there are likely a number of other factors, such as changes in air quality, lighting, pollutants, and so forth, that would impact mental health outcomes. In such a case, one would likely need a model that dynamically adjusts the relationship between greenspace

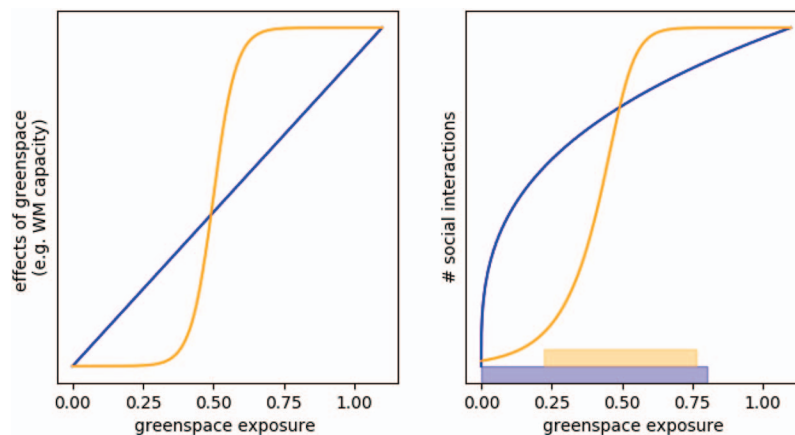


Figure 4. Coupling strength between greenspace and number of social interactions as mediated by neurocognitive improvements through greenspace exposure. Left: A linear (blue) and sigmoidal (orange) dose–response curve for hypothetical greenspace effects on neurocognitive functioning (e.g., WM capacity). Right: Depiction of the relationship between greenspace and the number of social interactions (as impacted by WM improvements) for two different greenspace neurocognitive-restoration dose–response curves. We can define the dynamic range as $\Delta = 10 \times \log_{10}(g_{90}/g_{10})$, where, for example, g_{10} is the greenspace exposure level when \bar{T} reaches 10% of its total response, g_{90} is the greenspace exposure level when \bar{T} reaches 90% of its total response, and the dynamic range Δ has units of decibels. A linear dose–response curve (blue line) results in a wide range (strong coupling, blue bar, $\Delta = 29$ db, $\bar{T} \sim g^{1/3}$) over which greenspace interacts with the number of social interactions. A sigmoidal dose response curve (orange line) results in a limited range (orange bar, $\Delta = 3.8$ db, $\bar{T} \sim (1/(1 + e^{-g}))^{1/3}$) over which greenspace interacts strongly with the number of social interactions. Outside of this limited range, there is weak coupling between greenspace and the number of social interactions. See the online article for the color version of this figure.

and social interactions, and the relationship between social interactions and mental health, as greenspace increases because of the number of additional mediating and moderating factors (e.g., air quality and exposure to pollutants).

In contrast, in the sigmoidal case, the range of impact of greenspace on social interactions is much more constrained, that is, between 0.25 and 0.75. Because of this compressed range, the differences between those environmental extremes may not be as pronounced and may not vary as much by other factors. For example, a treed urban area (0.25 greenspace coverage) and a treed suburban area (0.75 greenspace coverage) are likely more similar in their air quality than an industrial park and a forest. This may mean that a simpler model could be employed, because there may be fewer differences in other factors such as air quality, lighting, pollution, and so forth between the two environments over the dynamic range of greenspace exposure effects. This means that in the linear dose–response curve case, a fully interactionist model would be required. However, in the sigmoidal case, simpler nondynamic techniques, for example, hierarchical linear models, that take advantage of loose coupling between hierarchical levels could be used to study the dynamics for this loosely coupled case. For example, if one wanted to predict how depression incidence rates change as cities add more greenspace (Bratman et al., 2019), in the linear case, one would have to consider how air quality, pollution, lighting, and so forth all change with increased greenspace, versus the sigmoidal case, in which the range of greenspace types over which there is an effect is much more constrained, so a simpler model can be used that may not need to account for all of these other variables.

This example highlights two important advantages of the environmental neuroscience approach. First, explicitly considering the structure and organization of the external environment and incorporating it into multiscale models can lead to dynamics that would be overlooked by simpler approaches (i.e., the importance of identifying over what range the effects manifest). Second, unlike DST, environmental neuroscience stresses the importance of investigating when interactions between different scales are meaningful: It is the job of the environmental neuroscientist to empirically determine whether multiscale dynamics are meaningful to their specific research questions (i.e., is there loose or tight coupling between different levels of analysis?). This means that interactions and dynamics between layers of analysis are empirically and theoretically determined, and not focused on or ignored based on philosophical grounds.

What Are the Boundaries of Environmental Neuroscience?

As one can see, the field of environmental neuroscience is broad and has implications for many different behaviors.

The field's position at the intersection of cognitive neuroscience and environmental psychology might give one the impression that the field is trying to derive a model for all behaviors or a "model for everything." Despite the potential breadth of the field, environmental neuroscientists place a strong practical emphasis on the detailed quantification of the external environment, such as quantifying environmental features of greenspace, disorder, pollutants, safety, noise, and so forth in the external physical environment and their relation to brain dynamics and behavior. It is this rich quantification of the external environment and its relation to brain processes that sets the field of environmental neuroscience apart from other fields. As such, behaviors that can be understood and predicted without recourse to detailed quantification of the environment and without examining environmental effects on brain processes are outside of the purview of environmental neuroscience. The example of people's views on gun control was one example that we provided that would not fall under the umbrella of environmental neuroscience, though if studied from another perspective, such as trying to understand how population density and cognitive overload/underload (Esterman & Rothlein, 2019) impacted views on gun control, then this topic could fit within the field of environmental neuroscience.

Importantly, the field of environmental neuroscience does strive to develop quantitative models of the relationships between different levels of analysis that relate to behavior, such as (epi)genomic, neural, social and environmental levels of analysis, while drawing on ideas from hierarchical systems theory to model these relationships. This means that environmental neuroscience subscribes to the idea that it is useful to decompose large systems into smaller subsystems, and to study and manipulate those smaller systems in order to understand the overall system better (Smith & Sage, 1973). Consequently, measuring the coupling strength of these subsystems is of critical importance. This focus on quantifying coupling strength means that environmental neuroscientists study phenomena at multiple levels of analysis (e.g., different temporal and spatial scales). Thus, it is a goal of environmental neuroscience to build quantitative models of the external environment and its impact on brain processes to understand many behaviors. At present, though, many critical data sets do not exist, and therefore we hope that future environmental neuroscientists will begin collecting such multiscale data so that predictive and causal models can be built.

The defining feature of environmental neuroscience is the collection and detailed quantification of features of the external environment that affect brain processing and subsequent behavior. The field of environmental neuroscience puts the external physical environment at the forefront and requires its practitioners to measure and manipulate specific features of the external environment, be it exposure to

greenspace, disorder, noise, gothic architecture, pollutants, and so forth (Berman et al., 2019).

Conclusion

Environmental neuroscience focuses on developing models that can integrate data from neurobiological, cognitive, extended social network, and environmental experiments. Building these models of neurobiologically based, cognitive models of behavior is fundamental to environmental neuroscience's goals of predicting and explaining behavior using data from neurobiology, sociology, psychology, and epigenetics. Additionally, these models need to capture the temporal dynamics of environmental neuroscience processes. As discussed above, some work has been done in network neuroscience to interrogate the multiscale organization of networks, including temporal dynamics of community structure and explicitly linking microscale features of network organization to macroscale characteristics (Bassett & Sporns, 2017). However, more work is needed so that a general approach can be formalized. For now, hierarchy theory provides a useful guide that will help produce the types of data that future methods will require.

Environmental neuroscience considers the crucial interplay between multiple temporal and spatial scales in order to observe the impact of various environmental contexts on brain and behavior. The ability to measure temporal information at different scales (e.g., walking in a park for an hour vs. growing up next to a forest preserve) and integrating those data with data from varying spatial scales, such as greenspace exposure in one's neighborhood versus one's city, allow for the construction of new models that account not only for both spatial and temporal scales but also across different levels of analysis (e.g., epigenomic, neurobiological, cognitive, social and environmental) of the aforementioned hierarchical system.

Along with the construction of these new models, another important feature of environmental neuroscience is the goal to explain and causally predict behavior in healthy and clinical populations. This goal of prediction, and not simply causal explanation (Yarkoni & Westfall, 2017), will allow environmental neuroscientists the freedom to examine data sets that exist outside of the lab in real-world settings that lack experimental control but that have high ecological validity. Adhering to a more predictive model in environmental neuroscience would also allow researchers to predict behavioral phenotypes from these various spatial and temporal scales and inform on possible intervention methods. This would also help researchers to identify the mitigating neurocognitive deficits that may arise as a result of adverse environments and the ability to construct and maintain positive and enriching environments for those lacking access. This can possibly be achieved by building better and/or optimal environments for individuals, communities,

and neighborhoods based on empirical research and subsequent integrative models. Additionally, this could help alert public health policymakers about how certain pervasive environments (both social and physical) are affecting individuals, which could lead to reforms that promote a more environmentally conscientious stance on public health—specifically, public mental health.

In summary, environmental neuroscience stresses that brain function and behavior do not occur in a vacuum devoid of environmental influence and builds off of past work and ideas that have promoted this claim. As such, environmental neuroscience aims to specify and manipulate how different environments affect organisms on large spatial scales (e.g., the organization of a city) to small spatial scales (e.g., the amount of perceived fractalness in the environment), and from long temporal scales (e.g., a human life span) to short temporal scales (e.g., exposures on the order of seconds). Environmental neuroscience posits that these effects manifest in a coupled hierarchical system and that understanding the coupling strength between levels of analysis will yield great insights into understanding the causal mechanisms and the predictability of behavior.

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Received May 10, 2019

Revision received October 14, 2019

Accepted October 22, 2019 ■