The promise of environmental neuroscience

The physical and social environment that surrounds us has a profound impact on our brains and behaviour. This impact is so fundamental that a complete understanding of neural mechanisms cannot be developed without taking into account the extensive interactions between neurobiology, psychology, behaviour and the environment.

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Rodents raised in enriched environments have increased dendritic growth compared to rodents raised in depleted environments[1], which results in improved learning[1]. Male zebra finches exposed to another bird's song show differential epigenetic landscapes in auditory forebrain compared to males isolated from song[2], which relates to the ability to learn song. For humans, brief interactions with outdoor natural environments are associated with improved memory and attention compared to interactions with busy outdoor urban settings[3]. Factors of indoor environments also significantly affect human behaviour, such as indoor air quality, lighting, noise, etc. In particular, it has been shown that experimentally manipulating CO_2 exposure, ventilation and volatile organic compounds can significantly reduce cognitive performance[4]. Examining indoor environments is particularly important given the increasing amount of time that humans are spending indoors (for example, ~90% in North America[4]). Importantly, the physical and social environment that surrounds us does not equally affect individuals. For example, being an s/s genotype for the *5-HTTLPR* gene increases sensitivity to the presence or absence of maltreatment and neglect during development[5]. The burgeoning field of environmental neuroscience pursues these types of integrative studies to understand the qualitative and quantitative relationships between the external environment, neurobiology, psychology and behaviour. In the process, environmental neuroscience will attempt to develop unified theories, models and ways to enumerate the complex relationships between our biology, our psychology and our physical and social environment.

Environmental neuroscience challenges

The burgeoning field of environmental neuroscience is concerned with how the physical environment interacts with (i) brain, (ii) behaviour and (iii) the social environment and how the physical environment can be altered to improve psychological and physiological states. Social psychology and social neuroscience are interested in similar questions, where the environment consists of one's social, cultural and familial contexts or environments. Environmental neuroscience is devoted to studying aspects of the physical environment that include but are not limited to noise, greenspace, degree or intensity of urban development, crime, low-level perceptual features (for example, colours, contours, etc.), pollutants, lighting, temperature, etc., and how those physical environment features affect individuals and groups.

Examining Fig. 1, one can see aspects of the physical and social environment that are known to affect brain and behaviour. However, in humans, there is a gap between our understanding of neurobiological mechanisms at the cell, circuit and systems levels and our broad-scale theories of behaviour and environmental influences on behaviour. Currently, we do not have the experimental frameworks, tools or methods to link key areas of research (for example, environmental psychology, social psychology, neuroscience and epigenetics) because we cannot perform much of the epigenetic and neuroscience work on humans (because for the most part we cannot perform invasive brain procedures on humans) and we cannot completely replicate human-like social and physical environments in non-human studies. We can study other species in the wild and their complex interactions with their social and physical environments (for example, honeybees and voles in the wild) that relate to human behaviour, but we may also need to experimentally manipulate those environments in ways that humans have manipulated their physical environments to increase further understanding. Below we list the goals of environmental neuroscience that will help to connect these different areas of research and attempt to overcome these challenges.

Environmental neuroscience goals

To begin to overcome these challenges, environmental neuroscience has five major goals. The first goal, like that of environmental psychology, is to put the physical and social environment at the forefront and to connect environmental psychology research with neuroscience and epigenetics research even more strongly to conceptually and empirically 'bridge the gap' among fields. Toward this end, environmental neuroscience aims to identify functional brain states and networks that can be compared across species. This could be done with functional neuroimaging, in which researchers use global brain network signatures (such as global functional connectivity, nonlinear brain dynamics, brain network modularity, etc.) across species, even if the structure of brain anatomy is distinct. Once this gap is bridged, environmental neuroscience can expand into the fields of environmental psychology, neuroscience and epigenetics to answer such questions as to whether individual brain networks are differentially shaped by interactions with certain physical environments.

The second goal of environmental neuroscience is to identify the quantitative and qualitative relationships between the different levels of biological and environmental analyses, in support of new predictive models of behaviour. This entails defining parameters and relationships between variables for the expanded Lewin equation (i.e., behaviour = f(genetics, neurobiology, psychology, environment); Fig. 1) and using computational modelling techniques[6]. This will require going from more molar concepts to more molecular mechanisms and back. Importantly, this also means that the same objective stimulation from the physical environment may not be processed identically for different individuals[5] (for example, individuals with different genetic susceptibility and behavioural or experiential history), and social context will likely also affect how physical environment features are processed[7].

The third goal is to examine humans across the lifespan, as individuals are shaped by the accumulation of their experiences.
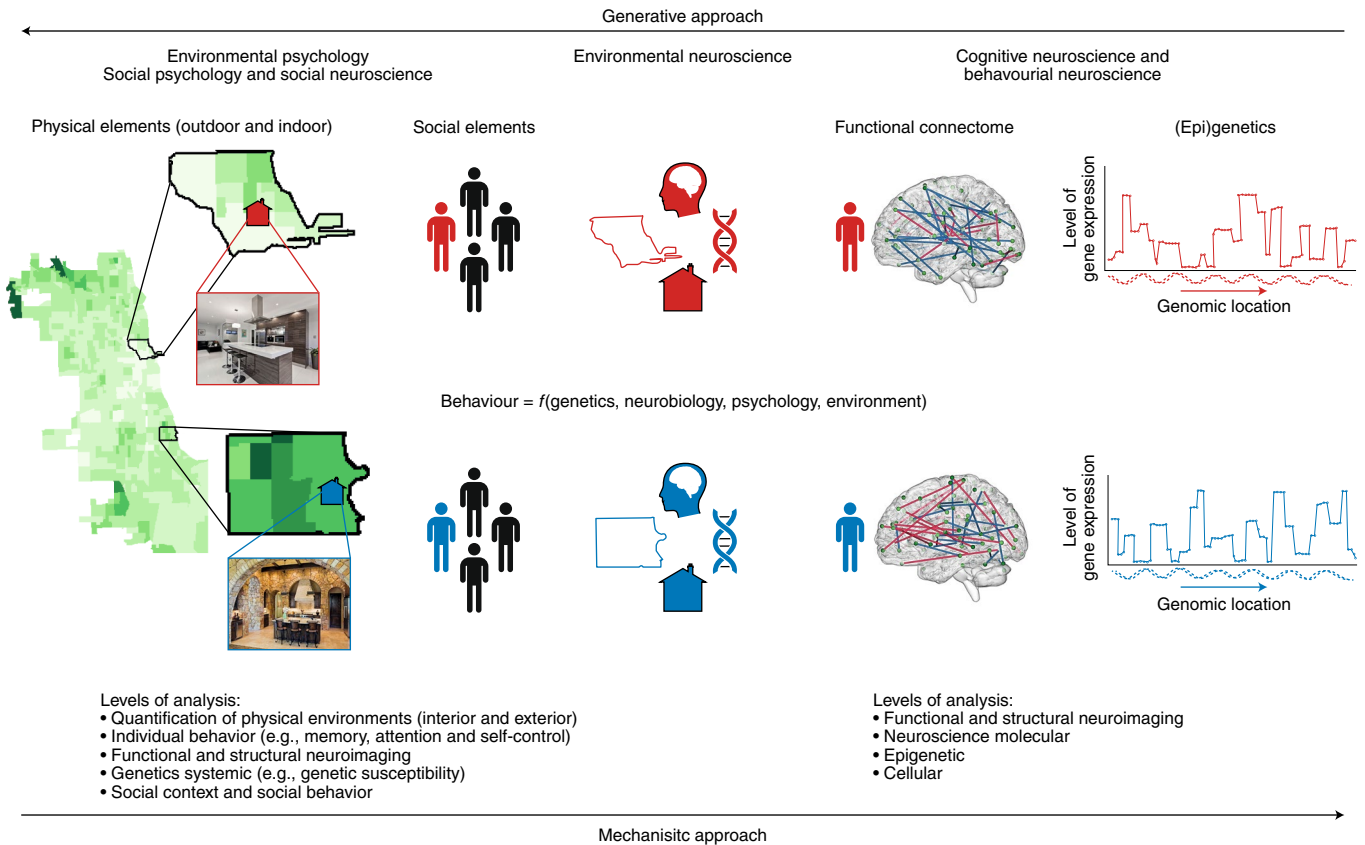
Fig. 1 | The elements of environmental neuroscience. Environmental neuroscience combines elements of environmental psychology; social and cognitive psychology; and social, cognitive and behavioural neuroscience to study how the physical and social environment interacts with our neurobiology to produce behaviour. From left to right are two neighbourhoods in Chicago that vary in their percentage of tree canopy (green), with darker green areas indicating a higher percentage. The indoor environments vary in architectural dimensions such as scaling and contrast that have been discussed extensively by the architect C. Alexander. The red-outlined indoor environment has less scaling and contrast than the blue-outlined indoor environment. All of these elements may affect social interactions, brain network behaviour (blue edges and lines indicate decreased functional connectivity; red edges and lines indicate increased functional connectivity) and gene expression. As K. Lewin proposed in the 1930s, human behaviour is f(person, environment). Environmental neuroscience aims to build models describing the quantitative and qualitative relationships between these levels of analysis and aims to expand Lewin's equation. Moving from left to right is the mechanistic approach to environmental neuroscience. Moving from right to left is the generative approach to environmental neuroscience. On this spectrum, environmental neuroscience is positioned in a manner enabling researchers to utilize neurobiology to design, test and manipulate different physical environments and vice versa. Figure icons made by Freepik from www.flaticon.com.

We know from epigenetic data that these experiences are reflected in our patterns of genomic function and that they affect brain processes and, subsequently, behaviour.

The fourth goal is to attempt to understand complex human physical and social environments in comparison with non-human species. This can be done in two ways. The first is to study other species' complex behaviours and interactions within physical and social environments that are similar to the interactions that humans have. This is already happening. The second is to alter the physical environment of other species to mirror ways that humans have altered their own physical environments, which we believe is another way to help bridge the gap between environmental psychology, social psychology, neuroscience and epigenetics, by creating physical

environments that are matched to one another. This, along with the second goal (of finding common global brain metrics across species), will also help to transition from the different levels of analysis.

The fifth goal of environmental neuroscience is to take a generative theoretical approach using results from (epi) genetics and neuroscience to design the physical environment to improve human psychological functioning. Environmental neuroscience not only attempts to uncover mechanistic explanations for more molar environmental effects, but also strives to use the more molecular and neurobiological results to design and test environments that may yield improvements for many different behaviours. To get at this generative goal, we will first need unified theories, models and ways to enumerate the complex

interrelationships between our biology and our physical environment.

The future
Research has shown that brief exposures to and interactions with natural environments, compared to interactions with busy urban environments, can lead to improvements in cognitive performance[3]. Importantly, these effects are not driven by mood[3] and may be partially driven by the sensory processing of low-level physical features of more natural vs. more urban environments[8], such as the amount of fractalness in the environment[9] or the amount of curved and straight lines[8]. In fact, simply processing disordered visual stimulation can cause lapses in self-control[8] and alter people's thought content. These are interesting effects, but we need mechanistic explanations for how these effects manifest

and how they relate to each other. Does perceiving certain physical patterns place the brain in more relaxed vs. effortful state[9]? Could prolonged perception of these features alter brain morphology? To answer that question, one would likely need to expose non-human animals to these types of stimulation for prolonged periods of time (for example, weeks or months) and examine alterations in brain structure and function. An environmental neuroscientist could attempt to create complex physical environments for non-human species that would mimic key features of human environments and/or leverage results from existing complex physical environments that other species face that share features with human environments. Creating human-like environments in other species has been attempted in the past, such as the work by John Calhoun and his 'rodent universe' to study the effects of crowding[10]. The interpretation of those findings is controversial, but the idea of creating human like environments for non-human species, while simultaneously collecting neural and behavioural measures that could be compared to humans would help to push the field of environmental neuroscience research forward. This along with leveraging research in other species interacting with their own complex physical and social environments will increase our understanding of the relationships between the physical environment, the social environment and neurobiology.

The above research implies that background processing of the physical environment can be fatiguing depending on the characteristics of the environment. Recently, Zenon and colleagues[11] composed a Bayesian information theoretic model that equates cognitive costs to the cost of converting external stimuli, X, to internal representations, Z, and then using these internal representations, Z, to choose some action, Y. Costs are incurred when there is a large divergence between an initial belief or prior compared to an updated belief or posterior probability after receiving new input. For example, urban environments may contain substantial unexpected stimulation with many fast-moving objects (for example, cars), people, noises and media, which may create large divergences between initial priors and updated internal representations, which could lead to cognitive costs. This model helps to capture how different levels of analysis, i.e., external environmental features and internal psychological representations, may interact and could lead to quantitative parameters in the expanded Lewin equation. Linking these computational models to neural

data will require data from environmental neuroscience to quantify the metabolic costs for representing external stimulation with internal neural representations.

Examining epigenetic effects is also a critical element of environmental neuroscience. Epigenetic mechanisms alter genomic function without altering the DNA sequence. Epigenetic mechanisms are regulated by the specific life experiences of an individual and are often stable. In this way, the environment itself can become part of the persistent biology of an individual, influencing which genes are made into the protein products that alter cell, neural network, and psychological functions. In other words, epigenetic mechanisms alter how current and future environments are processed based on prior environmental experiences because stable epigenetic modifications influence which genes can be produced in response to these experiences. Hundreds of investigations in humans and other species have demonstrated a link between experience and persistent effects on brain function and behaviour, including how people's epigenetic profiles reflect their childhood environments years after the experiences occurred[12]. Many of the environments discussed in those articles involve social stress, whereas environmental neuroscience would also ask questions about how long-term exposures to different physical environments might affect epigenetic mechanisms, which would then alter brain networks and behaviour. Recent work in zebra finches has shown that the ability to learn song is affected by exposure to song sensory input from male tutors in the environment during a critical period of development. This process is mediated by epigenetic transcriptional regulation, where exposure to bird song increases transcriptional regulation in auditory forebrain[4]. This work leads to questions about how exposure to different environmental factors such as ambient sound might affect learning. In addition, this work also informs how complex social interactions impact learning, as auditory learning in the zebra finch has a strong social component between male tutors and juvenile male learners. However, to link this non-human work to human work, one would need to utilize brain network measures that could be compared across species to link these epigenetic effects in brain tissue to humans (as referenced in the first goal of environmental neuroscience).

The field of environmental neuroscience aims to understand the biological mechanisms of the environment's effect

on behaviour. This is the mechanistic arrow in Fig. 1. In addition, the field of environmental neuroscience aims to use knowledge from neurobiology to design, test and generate environments that will improve human psychological functioning (this is generative arrow from Fig. 1). This will, of course, be complicated as individuals have different brains and different susceptibilities to the environment, so it is unlikely that there will be a 'universally' good environment. However, there may be enough consensus amongst individuals to create environments that would greatly improve human capabilities and psychological functioning at large scales. This may even mean dynamically altering the environment based on brain activity patterns to change lighting, temperature, etc. This will also require that environmental neuroscientists work with architects, builders and planners to determine what designs are feasible. Combining all of this science together will require unified theories, models and ways to enumerate these complex relationships to parameterize the expanded Lewin equation. We believe that the burgeoning field of environmental neuroscience will help to get us on that path. ❑

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Competing interests

The authors declare no competing interests.