

Ecological Brain: Reframing the Study of Human Behaviour and Cognition

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Abstract

The last decade has seen substantial advances in the capacity to record behaviour and neural activity in humans in real-world settings, to simulate real-world situations in laboratory settings and to apply sophisticated analyses to large-scale data. Along with these developments, the call for ecological validity (increased use of naturalistic materials and more real-world-like settings for experiments) has been renewed. Here we sketch a framework for real-world research where previous approaches are integrated into a cyclic process of “bringing the lab to the real world” (recording behavioural and neural responses in their real-world settings) and “bringing the real-world to the lab” (manipulating the environments in which behaviours occur in the lab) that allows for discovery and theory development.

Brain and Behaviour in the Real World and in the Lab

The human brain has evolved to survive in complex environments. We engage with and adapt our behaviours to who and what surrounds us. For example, to get from A to B, we may use external aids (e.g. GPS-guidance), or knowledge of the typical location of landmarks (e.g., tills to get out of a supermarket). If a place is particularly crowded, we may ask other people for help. Thus, the way we engage specific cognitive functions (e.g., navigation) depends on the specific environment. Yet, within psychology and cognitive neuroscience, the traditional approach to studying behaviour has involved experiments that do not incorporate the multiple, complex, and interrelated variables typical of real-world environments, nor the interplay between different cognitive functions in specific environments. Generally, cognition and behaviour have been mainly investigated within a **reductionist** (see glossary) practice. Reductionism prioritises parcellation of cognitive functions and control of environmental variables at the expense of accounting for human behaviour in the specific environments that characterise our daily lives. While this ensures that causal factors can be identified, their impact can be limited to those same conditions identified in the specific experiment which may differ from those in our everyday life.

Over the years many scholars have questioned this way of conducting scientific investigations and there have been calls for more naturalistic, real-world approaches to psychological and neuroscientific research (e.g., [1-18]). Especially in recent years, these calls have received increased interest due to the advent of new technologies that allow for mobile recording of behaviour and brain activity simultaneously, from multiple agents, and in-the-wild, as well as new analysis tools (e.g. [19-22]).

The push for increased real-world research has centred around the notion of ‘ecological validity’ (see Box 1). This concept, although used somewhat differently by different authors (see [23-25]), highlights the issue of generalisability from behavioural and neural responses elicited in the lab to those elicited in the real-world situations. Generalisability is still an implicit assumption, rarely tested in psychology and cognitive neuroscience. Even when the behavioural and neural mechanisms investigated in the lab and those in the real-world situations are highly similar, insufficient consideration of environmental elements can lead to faulty inferences and ill-posed questions/predictions about how humans behave. For example, different environments

may result in different behaviours, depending on what would be the most suitable (e.g., [26]), or 'optimal' (e.g., [27]) behaviour. As Kihlstrom [28] eloquently put it: *"The purpose of laboratory research is to understand the real-world: to make the problem simple so that it can be studied effectively, and to control relevant variables so that important relations, especially causal relations, can be revealed. Unfortunately, generalisation from the lab to the real-world requires an inferential leap: its legitimacy depends on the degree of similarity between the conditions that are obtained in the laboratory and those found in the real-world"* (pg 6).

To achieve generalisability to the real-world, researchers have advocated for the use of real-life complex and dynamic stimuli (e.g., [15, 16]), or, in addition, for the use of life-like settings (e.g., [10, 14]). For example, studies have brought experimental manipulations to real-world settings (e.g., [29]); and brought complex real-world settings into lab spaces (e.g., [30]). The Ecological Brain framework builds on these approaches and goes beyond by providing a general basis for theory building and discovery where research in the real-world and in the lab are integrated. Below, we first describe the Ecological Brain framework, its guiding principles and its implications, before providing a discussion of how the Ecological Brain framework can be implemented.

The Ecological Brain Framework

Ecological Brain provides a framework for rigorously capturing the complexity of human behaviour in interaction with the environment. It proposes a cyclic approach in which exploratory research in the real-world informs the design of lab experiments, particularly with respect to characterising environmental variables, but equally, hypotheses that are developed in the lab are validated in the real-world. This is extended in a continuous cycle of refinements and new hypothesis generation, leading to a new standard in research that cannot be achieved using real-world or lab studies alone (see Figure 1). In the Ecological Brain approach, by taking advantage of new emerging technologies and data analytics, we argue for a transfer of the *rigour* of laboratory studies into research in the wild (the real-world) and the *complexity* of the real-world into research in the laboratory in such a way that they can inform each other (Figure 1). It goes beyond the use of naturalistic stimuli and life-like settings and sets an agenda in which rigorous quantitative methods for the (exploratory) study of brain and behaviour *in the wild*

provide key insights about specific environmental aspects that need to be manipulated/controlled to allow for hypothesis testing in the lab. As it brings together research *in the wild* and *in the lab*, ecological validity is embedded in the cycling between the two approaches that forces a characterisation of the environment.

To bring the laboratory to the real world and vice versa, psychologists and neuroscientists are not enough. Ecological brain research must draw from different disciplines: those concerned with methodological and technological advances (e.g. computer science and medical physics) and, crucially, those concerned with the study and quantification of the environment (e.g. engineering, architecture, planning, geography). Importantly, the Ecological Brain approach differs from other **interdisciplinary** (see glossary) approaches (including human **ecology** – see glossary, behavioural ecology, environmental psychology, social geography, biological anthropology, population ecology, sociology and neuroethology) in that its interdisciplinarity specifically serves the objective of capturing the complexity of human behaviour, real-world environments and their *bidirectional* relationship. In other words, interdisciplinarity contributes to understanding how humans impact and are impacted by the surrounding environment, including the neural mechanisms engaged in this process. This means that research within the Ecological Brain Framework can go beyond understanding behaviour and its underlying brain functions per se, to exploiting this knowledge to improve the environment, in a way that can support human cognition and well-being.

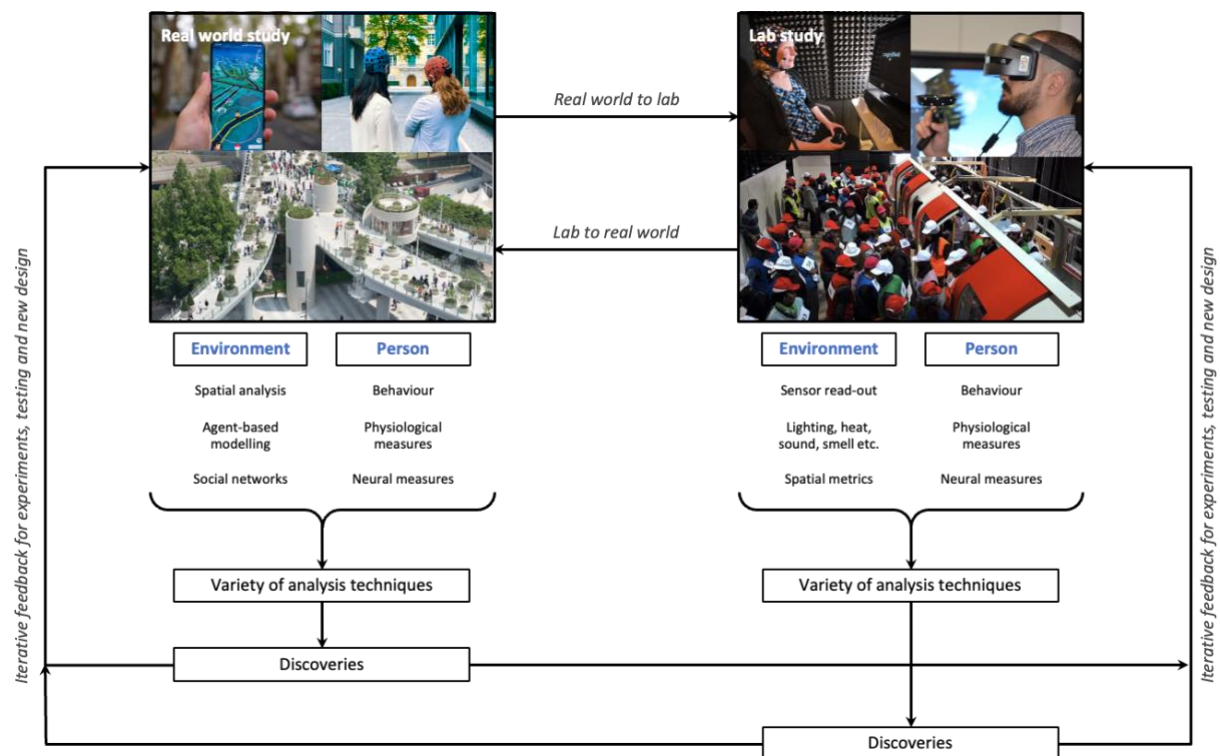


Figure 1 (Key Figure). A framework for the ecological study of human brain and behaviour.

Traditionally, research in ‘the wild’ is considered exploratory and descriptive with marginal bearing on theory development. Research in ‘the lab’ is considered as confirmatory and capable of testing theories. In lab research, stimuli are simplified and controlled, so the effects can be isolated to the particular aspects of the stimuli and/or task. Here, we illustrate how an ‘Ecobrain’ approach moves beyond this distinction to a cyclic research process in which real-world phenomena are identified and studied both in the real-world (left) and in the lab (right). Real-world research, with the use of mobile technologies for continuous recording of behavioural, physiological and neural activity, combined with data-driven modelling approaches, allows for identification of key environmental variables and for prediction of behavioural, physiological and neural responses. The lab, supplemented with technologies that allow for control of environmental variables, allows for theory testing in settings that embed key environmental variables identified in real-world research. Lab research can also provide new insights that can guide further research in the real-world. *Image credits: top left composite: EEG image reproduced with permission from Mentalab, contributors to making data acquisition in real-life scenarios possible. Seoul’s skygarden image, reproduced with permission from Ossip van Duivenbode. Top right composite: lab-based London Underground study image reproduced with permission from PEARL. All other images combined and reproduced with permission under the Creative Commons Attribution 4.0 International Licence.*

Core Features of Ecological Brain

Research must be exploratory and confirmatory

Research in the real-world is often considered exploratory and therefore useful for pilot studies, but overall less important than confirmatory hypothesis-driven research. However, exploratory research is necessary to identify key variables in novel areas of research, and to re-think known phenomena. Identifying relevant variables in the real-world is a necessary step for theory development, leading to hypotheses concerning

how these variables or their interactions would affect the phenomenon that can then be experimentally manipulated. Although conclusions drawn from exploratory research cannot identify causes and effects, they can define the problem space for hypothesis generation and can be rigorous by virtue of using best statistical practices. Because exploration is necessary to ground our studies in the real-world, it should be treated *au par and complementary*, with confirmatory lab-based research.

Theories must incorporate the environment

The goal of our theories is to identify general, possibly universal, principles underscoring human cognition at behavioural and neural levels. Historically, this effort has been primarily based on evidence from very homogeneous groups from Western countries. Differences within groups, both individual and cultural have now become an important part of our studies and theories [31-33]. However, other aspects of the physical and social environment also need to be considered and theoretically characterised. Otherwise, cognitive processes studied in isolated or highly specific tasks can only lead to the identification of specific principles of human behaviour as applied to the specific experimental setting. In the Ecological Brain framework, we argue for a theoretical characterisation of the diverse environments in which specific cognitive functions are used (e.g., wayfinding in a building, in a city, in a forest by individuals from different cultures) based on investigations in the real-world. The assumption is that it is only by developing such characterisations that we can identify the general (and possibly universal) principles of human behaviour.

Research methods must capture the environment

Our methods must allow us to measure the real-world variables of interest (e.g. [34]). In the Ecological Brain framework, the environment is not just the stage where our actors (experimental variables) play, but becomes an integral component of the performance. Therefore, operationalisations of the research question(s), hypotheses, and predictions have to include aspects of the physical, social, personal and cultural environment (e.g. [35]). This likely may involve using tools from other disciplines (e.g., geography, architecture, anthropology, see Figure 2). This approach can allow one to characterise relationships between different types of environment and generalise findings across environments, both vital components of theoretical advance.

Research must be interdisciplinary

To truly capture the *in situ* nature of complex behaviour, research must be interdisciplinary. Insights from disciplines concerned with the study of the physical environment, but also disciplines traditionally concerned with the study of humans in their natural environments must be taken into account during theory development, along with insights from cognitive science and neuroscience. Interdisciplinarity is also central at a methodological level for ensuring state-of-the-art methods in the implementation of Ecological Brain research (see Table 1). As already mentioned, these contributions are *bidirectional*, as it is not only the case that insights from other disciplines are necessary to better understand brain and behaviour, but also that a better understanding of brain and behaviour can lead to novel insights in the other fields.

How the Ecological Brain framework solves key problems with reductionism

The Ecological Brain framework provides the means to avoid the following general issues inherent to the standard reductionist approach.

The risk of partially blinded theories

Following reductionism, mental events are decomposed into distinct psychological processes (e.g., memory, language etc.), and further decomposed into more specific components (e.g., episodic, semantic and autobiographical memory). The separability and independence of different processes and sub-processes have been continuously debated (e.g., [36]). Crucially, theories based on this approach are linked to *operationalisations* that allow laboratory testing and research is limited to those psychological components that can be operationalised. While this is a major component of scientific practice, it can lead to myopic characterisations of phenomena. This is because the link between theoretical constructs and operationalisations is often left implicit. A prime example comes from social neuroscience. For decades, social cognition theories were based on operationalisation of ‘social’ as individuals observing a social situation while sitting alone in front of a computer screen or constrained in an fMRI scanner. As discussed elsewhere, this does not tell us much about social interaction [37, 38]. It only covers one small aspect of social experience, and cannot be generalised to typical real-world scenarios where we are engaged in social situations

rather than simply observing them. Thus, any theory developed purely on the basis of the above operationalisation is partially blinded as it relates to only one part of the phenomenon. In the Ecological Brain framework, by characterising phenomena in real-world environments, we are forced to develop multiple operationalisations for each theoretical construct, reducing the risk that our theories are partially blind.

What do we mean by “context”?

A core feature of experiments is that everything that is not manipulated or measured is part of the **context** (see Glossary). Context must be controlled but because it is outside of the experimental interest, it typically does not need to be characterised. What context is depends on the definition of the area of investigation and the theories/hypotheses being tested. Context can refer to other subprocesses, properties of the physical environment, the current psychological state of the subject, individual traits, the social setting of the experiment etc. [39]. Thus, ‘context’ loses precision as it is used as an umbrella term to refer to anything that is not central to the processes under investigation. For example, language comprehension has been broken down into component parts (e.g. phonological, syntactic, semantic processing) each of which is often studied on its own, while considering any other aspects - either local (e.g., syntax and semantics) or global (e.g., the physical and social setting of the linguistic interaction) - as *contextual* and therefore not only unimportant but ‘confounding’. But local and global factors affect language comprehension: language processing is predictive and uses contextual information at all levels [40, 41]. Some authors have tried to classify the different contexts; however, such classifications are limited and there is no agreement about what categories should be used [42, 43]. In the Ecological Brain framework, each context is specified, characterised and included among the experimental variables, precluding any ‘cherry picking’ of only those aspects of the environment that are in line with one’s theoretical preferences. The contextual variables included are those relevant to the real-world manifestation of a behaviour under scrutiny; the theoretical relevance of each can then be experimentally assessed.

The problem of non-replicability

Questions of generalisability are intrinsically linked to questions of **replicability** (see glossary). Lack of replicability has been attributed to methodological issues discussed at length elsewhere (e.g. [44, 45]). Better measurement tools and more data can

improve replicability, however, lack of replicability can also stem from a lack of ecological validity. A common research practice when replicating experiments is to generalise them to slightly different conditions, or people. Without understanding how contextual factors can affect the experimental findings, any small change in experimental tasks can potentially tap into a different combination of cognitive processes, giving rise to novel (unreplicated and possibly unreplicable) results. Ecological Brain provides a way to understand how specific processes are deployed in the real-world and how the lab conditions are linked to the real-world, thus improving replicability of findings.

Implementing the Ecological Brain Approach

Arguments for more ecologically valid approaches have been laid out throughout past decades [1, 9, 46]. This poses the question of why practices have not yet fully changed. The answer is likely to be because it is very challenging. First, it requires resources (technologies, facilities and interdisciplinary teams) that are not as easily available especially in research cultures that favour individual contributions over team efforts.

Second, it is the case that studies providing better approximation of real-world settings may involve complex designs and produce multidimensional data that is harder to interpret. In the Ecological Brain approach, cyclicity between exploratory “in the wild” and confirmatory “in the lab” studies is key to successfully dealing with such complexity (Table 1).

Table 1: A survey of methods for implementing the Ecological Brain Framework

A: Methods that allow to bring the lab to the real world		
Method	Description	Key Reference
(Mobile) electroencephalography (EEG)	Noninvasive recording of electrical activity of the brain	Mobile EEG in research on neurodevelopmental disorders: Opportunities and challenges [47]
(Mobile) functional near-infrared spectroscopy (fNIRS)	Noninvasive recording of brain activity detecting changes in blood flow	A review on the use of wearable functional near-infrared spectroscopy in naturalistic environments [48]

(Mobile) optically pumped magnetoencephalography (op-MEG)	Noninvasive recording of brain activity detecting magnetic fields produced by the brain's electrical currents	Moving magnetoencephalography towards real-world applications with a wearable system [49]
Global Positioning System (GPS)	Provides (real-time) geolocation and time information	Review of GPS travel survey and GPS data-processing methods [50]
Indoor tracking	Provides (real-time) geolocation via tracking devices (e.g. bluetooth)	Indoor Tracking: Theory, Methods, and Technologies [51]
(Mobile) electrodermal activity (EDA) / galvanic skin response (GSR)	Monitoring changes in the skin's electrical conductance, due to sweat production	Neighborhood environments influence emotion and physiological reactivity [52]
Heart rate (HR) / heart rate variability (HRV)	Monitoring average heart beats and variability between heart beats	Interoceptive ability predicts survival on a London trading floor [53]
(Mobile) eye-tracking	Monitoring real-time changes of eye gaze direction and duration	Head-mounted eye tracking: A new method to describe infant looking [54]
Mobile sensing using smartphones	Monitoring and extraction of a variety of information using sensors that are embedded in mobile phones.	The rise of people-centric sensing [55]
B: Methods that allow to bring the real world to the lab		
Virtual reality (VR)	Performing tasks in computer-generated environments	Can simulated nature support mental health? Comparing short, single-doses of 360-degree nature videos in virtual reality with the outdoors [56]
Augmented reality (AR)	Overlaying computer-generated aids onto real environments	Is that me?—Embodiment and body perception with an augmented reality mirror [57]
Manipulated and controlled physical environments	Reconstructing full-scale environments to minimise real-world unpredictability and enable experimental control	Train design features affecting boarding and alighting of passengers [58]
C: Data processing and modelling of real-world data		
Space Syntax	Theory and method for investigating relationships between society and space.	Ward layout, communication and care quality: Spatial intelligibility as a key component of hospital design [59]
Geographic Information System (GIS)	A spatial system to create, manage, analyse, and map location data (where) and attribute data (what).	Geo-EEG: towards the use of EEG in the study of urban behaviour [60]

Facial expression and movement analysis	Automatic facial behaviour analysis toolkit capable of facial landmark detection, head pose estimation, facial action unit recognition, and eye-gaze estimation with available source code for both running and training the models.	OpenFace 2.0: Facial Behavior Analysis Toolkit [61]
Longitudinal and cohort studies	Collecting multi-purpose data on a large sample to investigate relations between outcomes (e.g., health) and exposures (e.g., deprivation), often over time, in the general population and in subpopulations.	The role of neighbourhood greenspace in children's spatial working memory [62]
Data-driven agent-based models	By using data from real-world experiments, it is possible to build models describing the behaviour of individuals, groups, communities and cities.	An Introduction to Agent-based Modeling: Modeling Natural, Social, and Engineered Complex Systems with NetLogo [63]

Taking the Lab into the Real-world

Taking the lab into the real-world to observe phenomena as they naturally unfold can often call for different or novel protocols and methods (see Figure 2 and Table 1A). Researchers may need to follow their participants' actions in their natural environments, resulting in experimental sessions run in uncommon settings and/or at uncommon hours. Examples include studies where the 'lab' moved to people's bedrooms to capture their thoughts after being woken at night [64], to the streets of London where people's memory and brain activity were measured while they walked around [65], tracked via GPS to locations to test navigation [66], or a classroom where student-teacher interactions were observed and neural synchronisation studied to capture learning as it occurred [29]. Mobile brain and behavioural monitoring devices allow the flexibility required in these studies and rapid technical developments may allow even more ambitious paradigms to be developed [67]. Mobile smart-phone devices with a plethora of sensors also provide excellent opportunities such as the opportunity of on-device computation, including the implementation of machine learning algorithms for behaviour inference [68-70].

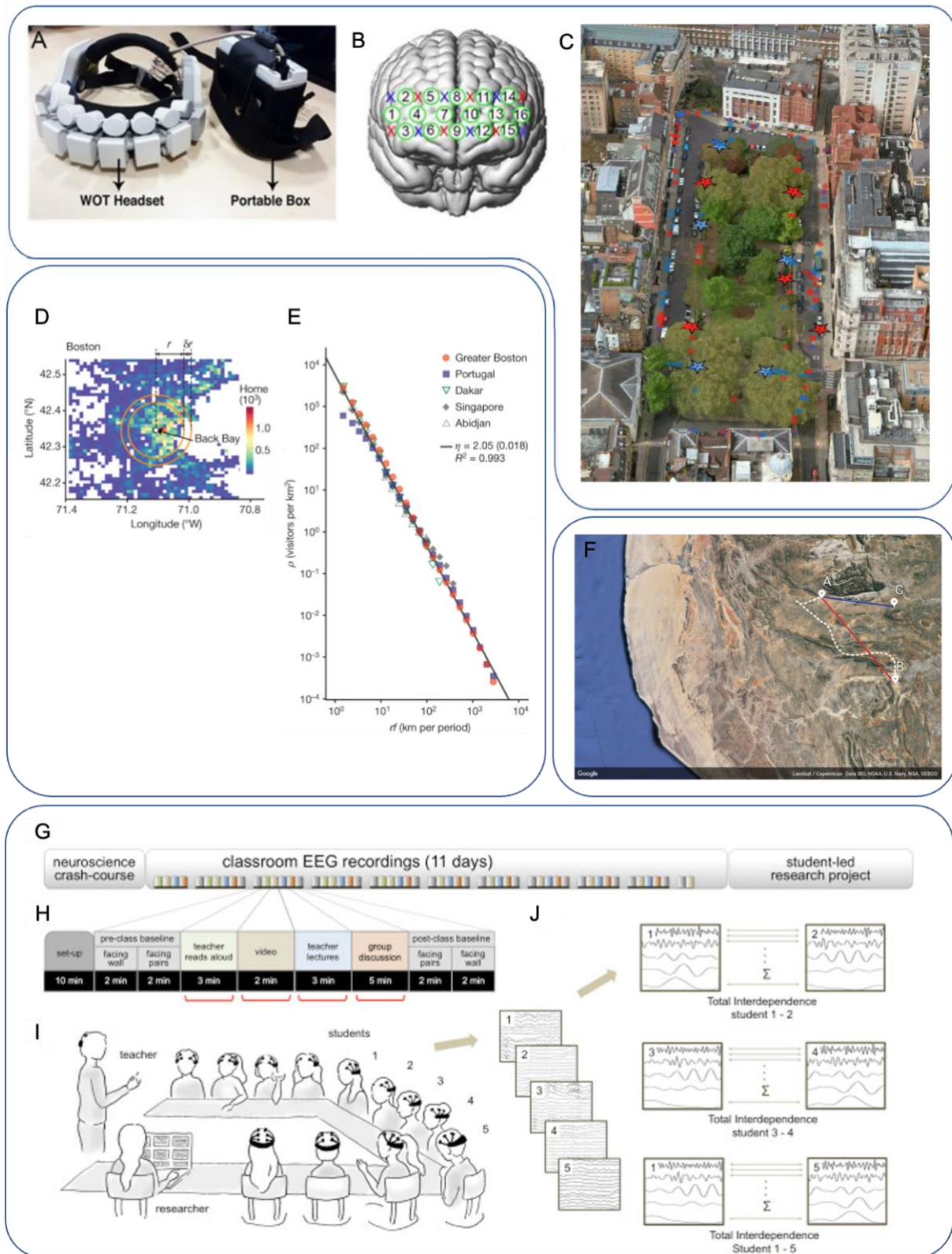


Figure 2. Taking the lab into the real-world. (A-C) Adapted from [71]. Functional near infrared spectroscopy (fNIRS) was used to record activity from participants walking in Queen Sq in London. (A) Recording device. (B) Sensors locations on the scalp to record prefrontal activity beneath. (C) Map of Queen Sq marking locations of social prospective memory cues (large blue stars), non-social prospective memory cues (large red stars), social functional haemodynamic events (blue asterisks), and non-social functional haemodynamic events (red asterisks). (D-E) Adapted from [72]. Large-scale mobility data from across the world is used to develop a scaling law that considers temporal and spatial dimensions of

human movement. (D). Map indicating population density in Black Bay, Boston, as deduced from mobile phone data. (E) Visitor flow is shown to depend on travel distance (r) and visiting frequency (f), with this scaling relation holding true for different urban regions around the world. (F) Adapted from [73]. Testing large-scale spatial ability; participants at location A point towards locations B and C, or imagine they are at location B and point to location C. (G-J) Adapted from [29]. EEG was used to record electrophysiological activity while students were engaged in classroom activities to explore brain-to-brain group synchrony and class engagement. (G-H) Experimental setup involved recording EEG activity of 12 students over 11 teaching days; red bars indicate individual EEG recording sessions. (I-J) 12 students wear EEG headsets to allow for brain-to-brain synchrony to be recorded. All images combined and reproduced with permission under the Creative Commons Attribution 4.0 International Licence.

Taking the Real-world into the Lab

Taking the complexity of the real-world to the lab allows for manipulation of environmental variables to establish their causal role. Virtual Reality (VR) and Augmented Reality (AR) enable people to experience highly controlled real-world-like environments at a low cost. Various studies have shown that findings in virtual worlds translate to findings in reality, making these methods particularly useful in terms of ensuring experimental control and ecological validity, whilst minimising costs and physical barriers to participating (e.g. [66]). Theatre-like research facilities can also provide remarkable real-world approximation, allowing us to reconstruct and adapt full-scale physical environments with a high level of precision and control (see UCL's Person Environment Activity Research Laboratory, PEARL). In Figure 3 we present examples of studies that reproduce in the laboratory key elements of complexity from the real-world. Table 1B, provides some of the methods for (re-)creating, controlling, and manipulating environments in the lab – both digitally and physically.

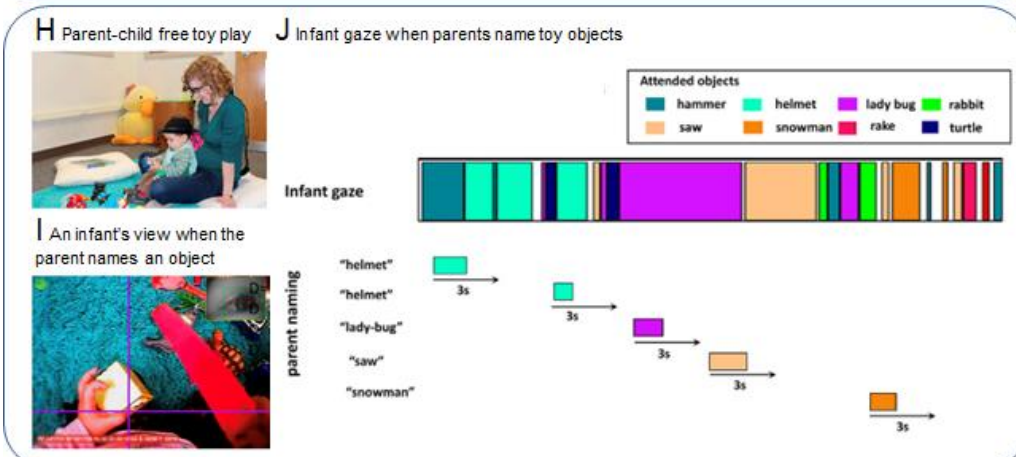
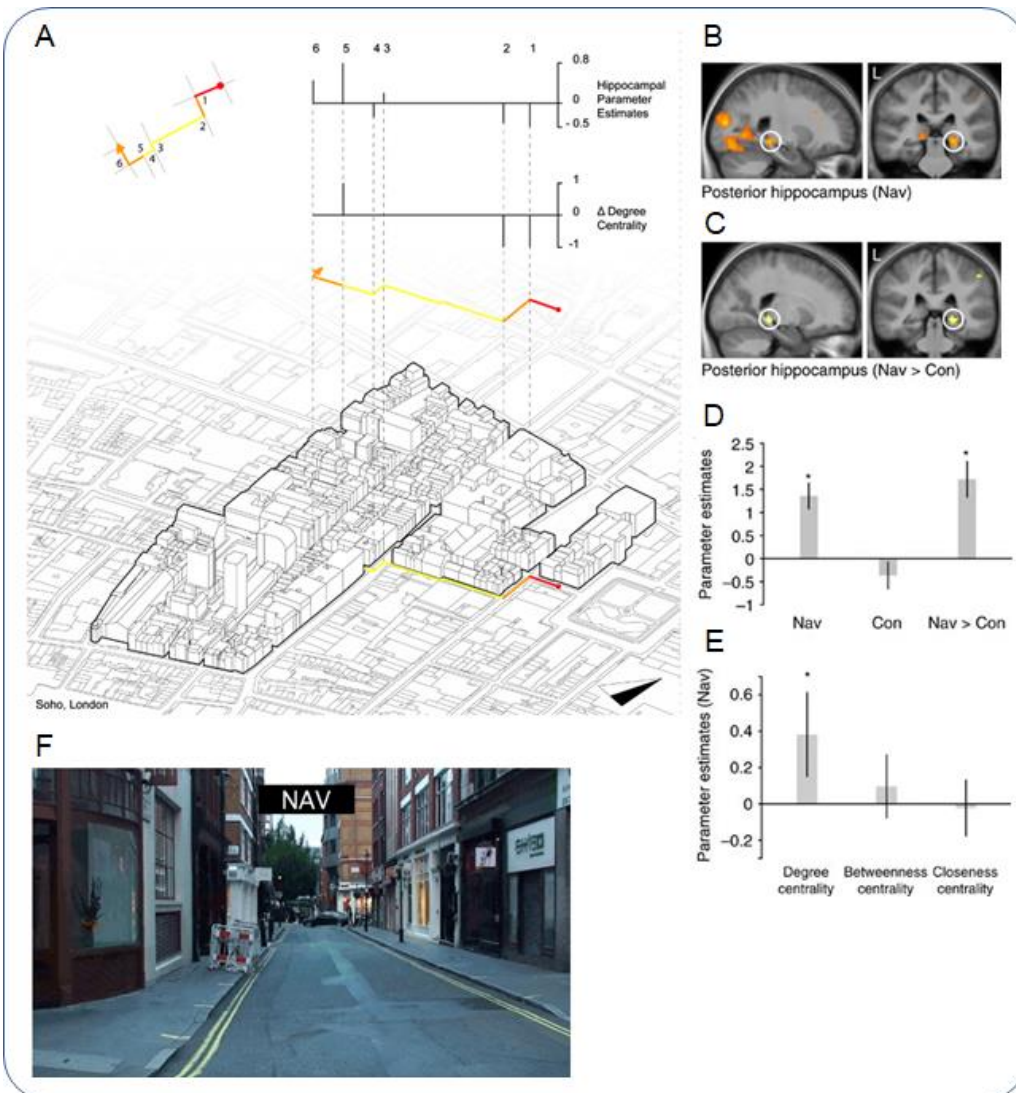


Figure 3. Taking the real-world into the lab. (A-F) Adapted from [30] and [74]. Graph theoretic analysis has been applied to street networks following a ‘space syntax’ approach based in architecture and urban data science. This analytical approach was combined with an fMRI BOLD data and film simulation of streets of Soho, in London (UK) to examine how the brain tracks spatial information during navigation. (A) Top left: degree centrality plotted for each street segment. Bottom: axonometric projection of the buildings on a map of Soho, with degree centrality projected above. Top right: change in degree centrality and right posterior hippocampus response at each individual boundary transition (1–6). (B,C) During Street Entry Events, right posterior hippocampal activity correlated significantly with the change in degree centrality for Navigation and Navigation>Control. (D) Parameter estimates in Navigation and Control conditions for mean activity in the right posterior hippocampus ROI for a model of degree centrality. Error bars denote the s.e.m. (E) Parameter estimates in the Navigation>Control condition for mean activity in the right posterior hippocampus ROI for a model containing degree centrality, betweenness centrality and closeness centrality. (F) A still from one of the movies used for the fMRI. (G) Images reproduced from <https://www.pearl.place>. Real-world environments are physically recreated at the PEARL facility to study tube carriages and greenspace respectively under controlled conditions. (H-J) Adapted from [75]. Head mounted cameras are used to study the link between infant’s attention and caregiver’s naming of objects in home-like environments. (H) Infants wear a head mounted camera whilst playing with toys freely with their parents. (I) Example of an infant’s gaze on an object when the parent names the object. (J) Infant gaze aligning with parent’s naming of objects, using a window of 3s from the onset of the object naming. Images combined and reproduced with permission under the Creative Commons Attribution 4.0 International Licence.

Analysing and Modelling Real-World Data

With more complex study designs, the data collected is also more complex. For example, during real-world wayfinding or navigation experiments, the researcher can control the start and end point of the route that a participant takes, and the task. Much more difficult to control are the unforeseeable events that occur en route e.g. cars, people, accidents, bad weather. Such variables can affect performance and thus need to be factored into the analysis. Mobile and personal technologies allow for collecting contextual multi-modal data (including social media data) describing the environments in which individuals act (e.g., [70]). From large longitudinal and cohort studies, to studies collecting data in real-time, data analytics can be used to explore how people, things, and places connect on a much larger scale, allowing for predictions of human behaviour that take into account the many concurring variables (see Table 1C).

Real-world data can also be used to develop a variety of data-driven agent-based models [63], which can be extended to represent complex models of multi-agent systems for studying groups, communities or cities [76]. These in silico simulations can be seen as a starting point to develop more concrete hypotheses from real-world patterns that can be then be tested in laboratory studies. An example is the problem of moral choice, which can be studied using simulated agents as a starting point for experiments involving humans [77].

Concluding Remarks

Ecological Brain provides a framework and a road-map for improving the generalisability of our studies to the real-world. While we believe reductionism has served psychology and cognitive neuroscience well as a principle for scientific research adherence to pure reductionism produces isolated and fragmented research. Many have argued that the assumption that mental events must be parcellated in order to be scientifically tractable cannot lead to a full understanding of brain-behaviour relationships (e.g., [78]), in Ecological Brain, how mental functions can be parcellated into processes and sub-processes is understood by investigating mental functions in their ecology.

More broadly, we join a growing number of other groups in arguing that understanding brain, behaviour and their relationship requires understanding how people function in their ecology (e.g., [5-8, 10, 12-15]). The environment, the context usually controlled in lab studies, cannot be dismissed *a priori*. We go beyond calling for more naturalistic stimuli and life-like tasks in experiments to proposing a continuous cycle between research in the real-world and in the lab combining: (i) mobile methods that allow for more exploratory studies designed to characterise brain and behavioural responses in specific real-world contexts and (ii) VR, augmented reality and other methods that allow for bringing those complex environmental variables (identified in real-world studies) in controlled laboratory settings. In the Ecological Brain approach, new discoveries come about as a consequence of the iteration between real-world and lab-based research (Figure 1).

Shifting how we study brain and behaviour can change how we describe/operationalise our object of investigation. For example, after Gibson [4, 79] introduced the concept of **affordances** (see Glossary), the ways in which scientists thought about vision was expanded. Instead of considering vision simply as a process of classification or categorisation, introducing affordances made vision an active process in which different visual stimuli carry different weight depending upon what they afford a person to do. We suspect shifting the focus of studying phenomena through the Ecological Brain framework can lead to questioning at least some existing tenants in the study of human cognition. In this way, the Ecological Brain framework may help the field to move beyond the current criticisms concerning methodological practices [80, 81], and lack of clear theoretical models [82].

It is important to acknowledge that conducting research that can be open-ended, data-driven, with multi-level data collection either outside the lab or in the lab with close-to-real-world conditions, is still challenging (see Outstanding Questions). There are however ways in which the scientific community can support a broader uptake of this approach. One way is by sharing preprocessed data acquired in the real-world (including code for processing and analysis as well as tools for reproducibility and for enabling further experiments). For example the Naturalistic Neuroimaging Database (<https://www.naturalistic-neuroimaging-database.org/>, Aliko et al. [83]) provide fMRI data from 86 participants each watching a full length movie that can be used to address a variety of questions (e.g., anxiety and amygdala connectivity, [84]). Datasets containing mobile sensing data of entire populations of individuals are also increasingly available. Examples include Reality Mining at MIT (<http://realitycommons.media.mit.edu/realitymining.html>) and StudentLife at Dartmouth (<https://studentlife.cs.dartmouth.edu/>). We strongly encourage others to make naturalistic datasets available as well as any code, and analytical tools (see e.g., <https://naturalistic-data.org/content/intro.html>) such that we can move closer to unravel the mysteries of the human brain and behaviour in its ecology.

Acknowledgments: Support for the development of the ideas reported here has been provided by the Leverhulme Trust (DS-2017-026; Doctoral Training Programme for the Ecological Study of the Brain). While writing this paper, GV was supported by an ERC Advanced Grant (ECOLANG 743035) and a Royal Soc Wolfson Research Merit Award (WRM\R3\170016).

Box 1: Ecological Validity

Ecological Validity is commonly used to refer to the extent to which results of a study have a bearing on real-world behaviour, both in terms of generalisability of the findings and their practical implications. Historically, Brunswik [85] defined ‘ecological validity’ in terms of the validity of *cues*, namely, the extent to which information available in the environment provides valid information about a distal stimulus, rather than the ecological validity of *experiments*, namely the extent to which experimental findings generalise to the “real world” situation that a researcher wishes to understand (see Holleman et al [23] for a discussion of Brunswik’s conception of ecological validity within the *lens model*). Orne [11] further elaborated this view focusing on the ecological validity of the experiments: the extent to which the experiment and the real-world present the same valid cues to the subject and therefore the *demand characteristics* of the experiment match those in the real-world (see [25], 2021). In recent years, ecological validity has been used to refer to the stimuli (i.e., emphasis on the use of more naturalistic materials) and/or the task (i.e., use of more life-like tasks). Both aspects are critical but insufficient to guarantee the ecological validity of a study: “An experiment can employ extremely life-like stimulus materials in an extremely lifelike setting... *But the experiment would still lack ecological validity if it also contained demand characteristics that are not present in the nonexperimental situation that it is intended to represent*” (Kihlstrom, 2021, p. 468-9).

GLOSSARY

Affordance: An affordance can be defined as a natural (i.e., not learnt) relationship between perceptual properties of the environment and relevant actions.

Context: This term is usually used to indicate aspects of a phenomenon that are not included in a theoretical account and are not manipulated in an experiment.

Interdisciplinarity: Interdisciplinarity analyses, synthesises and harmonises links between disciplines into a coordinated and coherent whole.

Reductionism: Reductionism, broadly defined as the practice of understanding more complex scientific phenomena in terms of smaller component parts, characterises much of the investigation across the experimental sciences. Within this framework, the notion of experimental control ensures that the phenomena under scrutiny are easily identifiable, scientifically tractable and specified to a point that affords the establishment of causal relationships.

Replicability: means obtaining consistent results across studies aimed at answering the same scientific question using new data or other new computational methods.

Ecology: The natural setting within which organisms develop, act and interact.

References

1. Brunswik, E., *Organismic achievement and environmental probability*. Psychological review, 1943. **50**(3): p. 255.
2. Brunswik, E. *Systematic and representative design of psychological experiments. With results in physical and social perception*. in *Proceedings of the [First] Berkeley symposium on mathematical statistics and probability*. 1949. University of California Press.
3. Chamberlain, A., et al. *Research in the wild: understanding in the wild approaches to design and development*. in *Proceedings of the Designing Interactive Systems Conference*. 2012.
4. Gibson, J.J., *The ecological approach to visual perception: classic edition*. 2014: Psychology press.
5. Hartley, C.A., *How do natural environments shape adaptive cognition across the lifespan?* Trends in Cognitive Sciences, 2022. **26**(12): p. 1029-1030.
6. Ibanez, A., *The mind's golden cage and cognition in the wild*. Trends in Cognitive Sciences, 2022. **26**(12): p. 1031-1034.
7. Jolly, E. and L.J. Chang, *The flatland fallacy: Moving beyond low-dimensional thinking*. Topics in cognitive science, 2019. **11**(2): p. 433-454.
8. Maguire, E.A., *Does memory research have a realistic future?* Trends in Cognitive Sciences, 2022.
9. Neisser, *Memory: What are the important questions*. Practical aspects of memory, 1978: p. 3-24.
10. Nastase, S.A., A. Goldstein, and U. Hasson, *Keep it real: rethinking the primacy of experimental control in cognitive neuroscience*. NeuroImage, 2020. **222**: p. 117254.
11. Orne, M.T., *ON THE SOCIAL-PSYCHOLOGY OF THE PSYCHOLOGICAL EXPERIMENT - WITH PARTICULAR REFERENCE TO DEMAND CHARACTERISTICS AND THEIR IMPLICATIONS*. American Psychologist, 1962. **17**(11): p. 776-783.
12. Spiers, H.J. and E.A. Maguire, *Decoding human brain activity during real-world experiences*. Trends in cognitive sciences, 2007. **11**(8): p. 356-365.
13. Rogers, N.T., et al., *Physical activity and trajectories of frailty among older adults: Evidence from the English Longitudinal Study of Ageing*. PloS one, 2017. **12**(2): p. e0170878.
14. Shamay-Tsoory, S.G. and A. Mendelsohn, *Real-life neuroscience: an ecological approach to brain and behavior research*. Perspectives on Psychological Science, 2019. **14**(5): p. 841-859.
15. Sonkusare, S., M. Breakspear, and C. Guo, *Naturalistic Stimuli in Neuroscience: Critically Acclaimed*. Trends in Cognitive Sciences, 2019. **23**(8): p. 699-714.
16. Snow, J.C. and J.C. Culham, *The treachery of images: how realism influences brain and behavior*. Trends in Cognitive Sciences, 2021. **25**(6): p. 506-519.
17. Hasson, U., et al., *Grounding the neurobiology of language in first principles: The necessity of non-language-centric explanations for language comprehension*. Cognition, 2018. **180**: p. 135-157.
18. Miller, C.T., et al., *Natural behavior is the language of the brain*. Current Biology, 2022. **32**(10): p. R482-R493.
19. Miller, G., *The smartphone psychology manifesto*. Perspectives on psychological science, 2012. **7**(3): p. 221-237.
20. Carpenter, S.M., et al., *Developments in mobile health just-in-time adaptive interventions for addiction science*. Current addiction reports, 2020. **7**: p. 280-290.
21. Wongvibulsin, S., et al., *An individualized, data-driven digital approach for precision behavior change*. American Journal of Lifestyle Medicine, 2020. **14**(3): p. 289-293.
22. Mobbs, D., et al., *Promises and challenges of human computational ethology*. Neuron, 2021. **109**(14): p. 2224-2238.

23. Holleman, G.A., et al., *The 'real-world approach' and its problems: A critique of the term ecological validity*. *Frontiers in Psychology*, 2020. **11**: p. 721.
24. Holleman, G.A., et al., *The reality of "real-life" neuroscience: a commentary on Shamay-Tsoory and Mendelsohn (2019)*. *Perspectives on Psychological Science*, 2021. **16**(2): p. 461-465.
25. Kihlstrom, J.F., *Ecological validity and "ecological validity"*. *Perspectives on Psychological Science*, 2021. **16**(2): p. 466-471.
26. Barron, A. and K.P. Schneider, *Variational pragmatics: Studying the impact of social factors on language use in interaction*. 2009.
27. Recarte, M.A. and L.M. Nunes, *Mental workload while driving: effects on visual search, discrimination, and decision making*. *Journal of experimental psychology: Applied*, 2003. **9**(2): p. 119.
28. Kihlstrom, J.F., *Demand characteristics in the laboratory and the clinic: Conversations and collaborations with subjects and patients*. *Prevention & Treatment*, 2002. **5**(1): p. 36c.
29. Dikker, S., et al., *Brain-to-Brain Synchrony Tracks Real-World Dynamic Group Interactions in the Classroom*. *Current Biology*, 2017. **27**(9): p. 1375-1380.
30. Javadi, A.-H., et al., *Hippocampal and prefrontal processing of network topology to simulate the future*. *Nature communications*, 2017. **8**(1): p. 14652.
31. Henrich, J., S.J. Heine, and A. Norenzayan, *The weirdest people in the world?* *Behavioral and Brain Sciences*, 2010. **33**(2-3): p. 61-+.
32. Blasi, D.E., et al., *Over-reliance on English hinders cognitive science*. *Trends in Cognitive Sciences*, 2022. **26**(12): p. 1153-1170.
33. Huppert, E., et al., *The development of children's preferences for equality and equity across 13 individualistic and collectivist cultures*. *Developmental Science*, 2019. **22**(2).
34. King, S.C., et al., *The effect of meal situation, social interaction, physical environment and choice on food acceptability*. *Food quality and preference*, 2004. **15**(7-8): p. 645-653.
35. Leve, L., et al., *Using a siblings reared apart and together design to study associations between parenting and child behavior problems*. *Behavior Genetics*, 2018. **48**(6): p. 488-489.
36. Westlin, C., et al., *Improving the study of brain-behavior relationships by revisiting basic assumptions*. *Trends in Cognitive Sciences*, 2023. **27**(3): p. 246-257.
37. Redcay, E. and L. Schilbach, *Using second-person neuroscience to elucidate the mechanisms of social interaction*. *Nature Reviews Neuroscience*, 2019. **20**(8): p. 495-505.
38. Hasson, U., et al., *Brain-to-brain coupling: a mechanism for creating and sharing a social world*. *Trends in Cognitive Sciences*, 2012. **16**(2): p. 114-121.
39. Nadel, L. and J. Willner, *CONTEXT AND CONDITIONING - A PLACE FOR SPACE*. *Physiological Psychology*, 1980. **8**(2): p. 218-228.
40. Heilbron, M., et al., *A hierarchy of linguistic predictions during natural language comprehension*. *Proceedings of the National Academy of Sciences of the United States of America*, 2022. **119**(32).
41. Zhang, Y., et al., *More than words: word predictability, prosody, gesture and mouth movements in natural language comprehension*. *Proceedings of the Royal Society B-Biological Sciences*, 2021. **288**(1955).
42. Meteyard, L. and G. Vigliocco, *Lexico-semantics*. *The Oxford handbook of psycholinguistics*, 2018: p. 71-90.
43. Cai, Z.G. and G. Vigliocco, *Word processing*. *Stevens' Handbook of Experimental Psychology and Cognitive Neuroscience*, 2018. **3**: p. 1-36.
44. Ioannidis, J.P.A., *Why most published research findings are false*. *Plos Medicine*, 2005. **2**(8): p. 696-701.
45. Ioannidis, J.P.A., *How to Make More Published Research True*. *Plos Medicine*, 2014. **11**(10).

46. Brunswik, E., *REPRESENTATIVE DESIGN AND PROBABILISTIC THEORY IN A FUNCTIONAL PSYCHOLOGY*. Psychological Review, 1955. **62**(3): p. 193-217.
47. Lau-Zhu, A., M.P.H. Lau, and G. McLoughlin, *Mobile EEG in research on neurodevelopmental disorders: Opportunities and challenges*. Developmental Cognitive Neuroscience, 2019. **36**.
48. Pinti, P., et al., *The present and future use of functional near-infrared spectroscopy (fNIRS) for cognitive neuroscience*. Annals of the New York Academy of Sciences, 2020. **1464**(1): p. 5-29.
49. Boto, E., et al., *Moving magnetoencephalography towards real-world applications with a wearable system*. Nature, 2018. **555**(7698): p. 657-+.
50. Shen, L. and P.R. Stopher, *Review of GPS Travel Survey and GPS Data-Processing Methods*. Transport Reviews, 2014. **34**(3): p. 316-334.
51. Dardari, D., P. Closas, and P.M. Djuric, *Indoor Tracking: Theory, Methods, and Technologies*. Ieee Transactions on Vehicular Technology, 2015. **64**(4): p. 1263-1278.
52. Hackman, D.A., et al., *Neighborhood environments influence emotion and physiological reactivity*. Scientific Reports, 2019. **9**.
53. Kandasamy, N., et al., *Interoceptive Ability Predicts Survival on a London Trading Floor*. Scientific Reports, 2016. **6**.
54. Franchak, J.M., et al., *Head-Mounted Eye Tracking: A New Method to Describe Infant Looking*. Child Development, 2011. **82**(6): p. 1738-1750.
55. Campbell, A.T., et al., *The rise of people-centric sensing*. Ieee Internet Computing, 2008. **12**(4): p. 12-21.
56. Browning, M., et al., *Can Simulated Nature Support Mental Health? Comparing Short, Single-Doses of 360-Degree Nature Videos in Virtual Reality With the Outdoors*. Frontiers in Psychology, 2020. **10**.
57. Nimcharoen, C., et al., *Is That Me?-Embodiment and Body Perception with an Augmented Reality Mirror*. in *17th IEEE International Symposium on Mixed and Augmented Reality (ISMAR)*. 2018. Munich, GERMANY.
58. Thoreau, R., et al., *Train design features affecting boarding and alighting of passengers*. Journal of Advanced Transportation, 2016. **50**(8): p. 2077-2088.
59. Pachilova, R. and K. Sailer. *Ward layout, communication and care quality: Spatial intelligibility as a key component of hospital design*. in *Proceedings of the 12th International Space Syntax Symposium*. 2019. International Space Syntax Symposium.
60. Mavros, P., M.Z. Austwick, and A.H. Smith, *Geo-EEG: Towards the Use of EEG in the Study of Urban Behaviour*. Applied Spatial Analysis and Policy, 2016. **9**(2): p. 191-212.
61. Baltrusaitis, T., et al. *Openface 2.0: Facial behavior analysis toolkit*. in *2018 13th IEEE international conference on automatic face & gesture recognition (FG 2018)*. 2018. IEEE.
62. Flouri, E., E. Papachristou, and E. Midouhas, *The role of neighbourhood greenspace in children's spatial working memory*. British Journal of Educational Psychology, 2019. **89**(2): p. 359-373.
63. Wilensky, U. and W. Rand, *An introduction to agent-based modeling: modeling natural, social, and engineered complex systems with NetLogo*. 2015: Mit Press.
64. Spano, G., et al., *Dreaming with hippocampal damage*. Elife, 2020. **9**.
65. Pinti, P., et al., *Using Fiberless, Wearable fNIRS to Monitor Brain Activity in Real-world Cognitive Tasks*. Jove-Journal of Visualized Experiments, 2015(106).
66. Coutrot, A., et al., *Global Determinants of Navigation Ability*. Current Biology, 2018. **28**(17): p. 2861-+.
67. Pentland, A. and A. Liu, *Modeling and prediction of human behavior*. Neural Computation, 1999. **11**(1): p. 229-242.
68. Choudhury, T., et al., *The mobile sensing platform: An embedded activity recognition system*. Ieee Pervasive Computing, 2008. **7**(2): p. 32-41.

69. Rachuri, K.K., et al. *EmotionSense: a mobile phones based adaptive platform for experimental social psychology research*. in *Proceedings of the 12th ACM international conference on Ubiquitous computing*. 2010.
70. Wang, R., et al. *StudentLife: assessing mental health, academic performance and behavioral trends of college students using smartphones*. in *Proceedings of the 2014 ACM international joint conference on pervasive and ubiquitous computing*. 2014.
71. Burgess, P.W., et al., *Prefrontal cortical activation associated with prospective memory while walking around a real-world street environment*. *NeuroImage*, 2022. **258**: p. 119392.
72. Schl pfer, M., et al., *The universal visitation law of human mobility*. *Nature*, 2021. **593**(7860): p. 522-527.
73. Davis, H.E., J. Stack, and E. Cashdan, *Cultural change reduces gender differences in mobility and spatial ability among seminomadic pastoralist-forager children in northern Namibia*. *Human Nature*, 2021. **32**(1): p. 178-206.
74. Gregorians, L. and H.J. Spiers, *Affordances for spatial navigation*. *Affordances in Everyday Life: A Multidisciplinary Collection of Essays*, 2022: p. 99-112.
75. Yu, C., et al., *The infant's view redefines the problem of referential uncertainty in early word learning*. *Proceedings of the National Academy of Sciences*, 2021. **118**(52): p. e2107019118.
76. Batty, M., *The new science of cities*. 2013: MIT press.
77. Tennant, E., S. Hailes, and M. Musolesi, *Modeling Moral Choices in Social Dilemmas with Multi-Agent Reinforcement Learning*. arXiv preprint arXiv:2301.08491, 2023.
78. Pessoa, L., *The entangled brain: How perception, cognition, and emotion are woven together*. 2022: MIT Press.
79. Gibson, J.J., R. Shaw, and J. Bransford, *Perceiving, acting, and knowing: Toward an ecological psychology*. 1977, Erlbaum, NJ.
80. Button, K.S., et al., *Power failure: why small sample size undermines the reliability of neuroscience*. *Nature reviews neuroscience*, 2013. **14**(5): p. 365-376.
81. Open, S.C., *Psychology. Estimating the reproducibility of psychological science*. *Science*, 2015. **349**(6251): p. aac4716.
82. Muthukrishna, M. and J. Henrich, *A problem in theory*. *Nature Human Behaviour*, 2019. **3**(3): p. 221-229.
83. Aliko, S., et al., *A naturalistic neuroimaging database for understanding the brain using ecological stimuli*. *Scientific Data*, 2020. **7**(1): p. 347.
84. Kirk, P.A., O.J. Robinson, and J.I. Skipper, *Anxiety and amygdala connectivity during movie-watching*. *Neuropsychologia*, 2022. **169**: p. 108194.
85. Brunswik, E., *Perception and the representative design of psychological experiments*. 1956: Univ of California Press.