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Big behavioral data: psychology, ethology and the foundations of neuroscience

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Behavior is a unifying organismal process where genes, neural function, anatomy and environment converge and interrelate. Here we review the current state and discuss the future effect of accelerating advances in technology for behavioral studies, focusing on rodents as an example. We frame our perspective in three dimensions: the degree of experimental constraint, dimensionality of data and level of description. We argue that 'big behavioral data' presents challenges proportionate to its promise and describe how these challenges might be met through opportunities afforded by the two rival conceptual legacies of twentieth century behavioral science, ethology and psychology. We conclude that, although 'more is not necessarily better', copious, quantitative and open behavioral data has the potential to transform and unify these two disciplines and to solidify the foundations of others, including neuroscience, but only if the development of new theoretical frameworks and improved experimental designs matches the technological progress.

Behavior is foundational

Behavior is what animals do. It can be defined as the muscular output of an organism or as its externally observable dynamical features (**Box 1**). The brain is the chief architect, orchestrator and driver of behavior; behavior, in turn, is the principal function of the brain. Thus, if the problem of neuroscience is to understand brain function, then success hinges not only on explaining how neural systems work, but in linking this to behavior in a systematic way. Thus, behavioral data is not simply a tool for helping neuroscientists interpret brain data, but also the foundational problem of neuroscience.

In their pursuit of a tractable problem, neuroscientists have tended to reduce the complexity of behavior by favoring highly constrained experimental preparations that allow them to focus on the complexity of the brain itself. However, behavior is as complex as the nervous system. Even knowing all possible details about genes or neurons would be incomplete if we could not relate them to behavior. Any 'omics' will ultimately miss the very point of the brain without this foundation (for example, natural selection acts on behavior, not directly on genes and neural firing patterns). Furthermore, it is not the brain alone that produces behavior, but rather its interaction with an even more complex and changing environment. Behavior is a particularly hard problem. It is a complex, highly dimensional, dynamical and relational phenomenon with no clear separation of scales. It is the unifying space in which genes, neural structure, neural function, body plan, physical constraints and environmental effects converge. Behavior is a natural continuum in which some of the most challenging questions of physics, biology, psychology and the social sciences converge.

The study of behavior has a long and rich history that we must try to summarize to frame our view of the future. Darwin proposed that behavior is selected through evolution[1], implying that behavioral units or patterns are encoded biologically and expressed in future generations (comparable across individuals) and in closely related species (comparable across species). In the nineteenth and twentieth centuries, two main lines of approach brought us to the modern age. On one side, the ethologists developed efforts to understand behavior in natural environments[2–4], seeking principles of organization of primarily innate behaviors[3] and common rules governing behavior across species. This led to concepts such as imprinting and releasing mechanisms[2,3]. They also developed methods to define how behavior patterns are composed of simpler interconnected parts (ethograms) and sought to describe the whole behavioral repertoire of a species, what we might call ethomes. In a second stream, mainly within physiology and psychology, behavior was studied in less natural and more controlled laboratory settings. These schools, including the behaviorists, developed paradigms primarily focused on learned behaviors relating stimuli, actions and outcomes, including classical conditioning[5] and instrumental or operant conditioning[6]. Their search for general principles of learning and motivation led to the development of principles including drive satisfaction[7], the generation and selection of behaviors on the basis of their consequences[8,9], and the formation and use of cognitive maps by which novel solutions can be deduced from experience[10–12].

We stand on these giant shoulders with a sense of progress, but without a glimpse of the horizon. Where are we going? From the similarities and differences between these prior efforts, we can define three primary axes in which to frame our discussion about the goals, limits and future opportunities for behavioral studies, especially in the light of the recent technological advances contributing to big behavioral data (BBD). **Figure 1** depicts this conceptual space, which is the backbone of our discussion: the legacy of previous studies (constraints), the main promise of BBD (dimensionality) and the challenges faced in applying it (description). For instance, relaxed constraints on animal behavior in naturalistic conditions recorded at low dimensionality via beam break events can be constrained much further in a two-alternative forced choice (2AFC) head-fixed preparations with lick events as measurement, whose

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Box 1 Behavior: definition and key features

Animal behavior is the macroscopic expression of neural activity, implemented by muscular and glandular contractions acting on the body, and resulting in egocentric and allocentric changes in an organized temporal sequence. Although we focus on rodents, behavior across all species is an expansive concept, ranging from speech, gestures and writing to micropostural adjustment, reaching and locomotion, from facial expressions, sneezing and crying to flying, diving and sonar emissions, not to mention construction of burrows, webs, buildings and bibles, and meditation. There are three important attributes of animal behavior.

First, behavior is relational. It is the confluence of an embodied brain with its environment. The relationship of the animal to the world (including other animals) defines affordances (opportunities for behaving), which are necessary for explaining and understanding behavior. This implies the need to specify the context (environment or assay) in which the behavioral phenomenon is defined. Approaches that formulate what is meaningful from the animal's point of view are attempts to grasp such relational aspect of animal behavior.

Second, behavior is dynamic. It is a process in which change is both accidental and essential. Physiology is distinguished from anatomy by dynamics; behavior is manifested both in space and time. Thus, time series analysis is critical to behavioral science. Even to speak of 'a behavior', as opposed to 'behavior', implies the replacement of a continuous trajectory by a symbol, token or word, which itself is a non-trivial inference. Theories and frameworks that address the continuous process of becoming can greatly advance our understanding dynamics in animal behavior.

Third, behavior is high dimensional. It appears complex and variable (unpredictable). The number of behavioral effectors and their degrees of freedom (for example, arm or vocal articulation) somewhat reduces the dimensionality compared to the brain itself, but the number is large enough that we cannot even clearly enumerate it. Bodies limit the simultaneous expression of incompatible behaviors (for example, go left implies not going right), but do not rule out concurrent manifestation of multiple behaviors (for example, talking and walking). Dimensionality reduction techniques are therefore decisive in the study of animal behavior.

dimensionality can in turn be increased by acquiring high-speed video data, from which further analysis can detect whisker position and choice. In a more naturalistic assay in which current technology allows to record animal behavior at high-resolution via ultrasonic microphones and video, the animal position and vocalizations can be extracted to, finally, infer the animal's emotional state or its uncertainty about the world in what represents a high level of description. Thus, we can map the activity in the behavioral space along the constraint, dimensionality and description dimensions to the legacy of psychology and ethology, the promise of BBD and the current challenges of behavioral neuroscience. We argue that the issue of constraints is an old conceptual struggle that remains unresolved, that moving to higher levels of description while reducing dimensionality remains a universal scientific motive, but one that is also dangerous when premature, and that the technology delivering BBD has enlarged the 'playing field' in ways that interact with the first two points.

Our primary aim is to articulate whether and how BBD can change the landscape of behavioral studies, considering the implication of this for the development of behavioral assays and constraints, and the possible need to revise old behavioral concepts and the possibility of paradigm shifts. We do so through the primary lens of rodent behavioral studies while bringing comparisons to other species and other 'omics' when useful, stressing the implications for the interpretation of neural data. We first review the tools and technology that are contributing to BBD and the promise for behavioral studies that they represent. We then discuss the challenges inherent in applying those tools in a scientifically productive manner. Next, we offer a more specific vision of how BBD approaches can transform modern versions of the psychological and ethological approaches, turning those challenges into opportunities for progress. We conclude with our view of the longer term effect of BBD on the future of neuroscience.

The promise: advances in technology

Human observation has been the standard approach to studying behavior for centuries. The advent of technology for acquiring records of these observations (photography, videography, etc.) found immediate application. More than just a tool for documenting observations, they offer access to new spatial and temporal scales that are inaccessible to an unaided human eye[13] (high-speed video, ultrasonic microphony, infrared illumination, etc.). Such augmented observations have become vital to many domains of behavioral neuroscience, yet they have historically been the pursuit of specialists requiring sophisticated, expensive equipment. Fortunately, driven by consumer interest in documenting the behavior of their children, cats and extreme sports mishaps, this technology has become much more accessible. It is now feasible and inexpensive to acquire, store and analyze vast amounts of behavioral data of extremely detailed audio and video records of animal behavior, continuously, for an entire experiment and in an automated manner. Currently, a full video record of a rodent's lifespan (~24 months) in a standard cage (millimeter resolution), at VGA resolution, day and night (infrared LED illumination) and lossy, yet sufficient, compression, can be acquired with a $50 webcam and stored on a hard drive.

Not restricted to standard media (audio, visual) modalities, sensors developed for smartphones (accelerometers, gyroscopes, GPS, etc.) can provide new measures of behavior in a robust, miniaturized package. Designed to operate at low power in wireless devices, these sensors can be affixed to an animal and transmit detailed, continuous measures of behavior over long times periods. Inertial sensors (accelerometers) have been used to extract continuous acceleration data from animal bodies, including humans, with high temporal resolution and long durations[14,15]. Furthermore, measurements from different types of sensors can be combined to infer more accurate measures[16]. For example, when combined with a geocentric reference and corrected for sensor drift, high temporal–resolution velocity and position data can be computed by integrating acceleration. The same microprocessors that make wireless transmission of inertial data possible also permit the sampling of other data sources. Any signal that can be turned into an analog voltage can be mated with a wireless system, allowing continuous wireless sensing of behaviorally relevant physiological signals such as body temperature, respiration via pressure or nasal temperature[17], heart rate and electromyogram, as well as with neural recordings[15,18].

Historically, a major constraint in the amount of behavioral data acquired has been the human resources required to perform each experiment. Advances in technology have made it increasingly feasible to automate the behavioral assay and thereby collect more animal data, important issues to which we will return. Automation of assays affords the substantial advantage of greater inter-laboratory reproducibility once committed to a given set of constraints implied by a uniform behavioral setup. These approaches have already seen substantial application in smaller species and have proven valuable for rodent studies[19]. Automation has been deployed on two levels. First, it has reduced the need for human monitoring and intervention, even that carried out remotely or offline[20]. These systems still require manual transfer of animals into and out of cages, etc. Second, 'live-in' systems in which rodents live in the behavioral assay or shuttle between home cage and assay by themselves[21] have also been automated. Commercial systems have integrated RFID technology with sensors

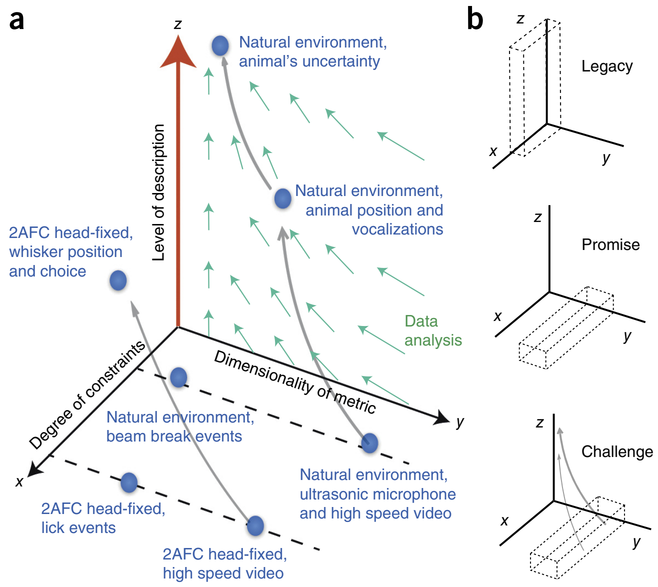

Figure 1 Conceptual representation of three main axes in the behavioral science space and their relationship to the legacy, promise and challenges of big behavioral data. (**a**) Experimental constraints (*x* axis), measurement dimensionality (*y* axis) and level of description (z axis). The degree of constraints is imposed by the experimental context: low in the case of ethologists, higher in the case of the psychologists. Constraints provide a frame of reference, expressing hypotheses about what is important to observe. They limit the scope of behavior, narrowing the expression possibilities to a particular set of conditions, and at the same time dictating the affordances available to the animal (for example, climbing can only be expressed in an environment that affords climbing). The precision and dimensionality of the records of classical ethologists and psychologists was limited to low-dimensional data available by direct observation, note taking, etc. The development of computer and information technology offers the possibility of larger, more precise, higher dimensional observations. The level of description ranges from the complexity of primary data (low level) to abstract metrics and general concepts (high level). Blue dots serve as different interrelated examples. (**b**) Legacy, promise and challenges of big behavioral data. The legacy, inherited from twentieth century ethology and psychology, is schematized in the constraints-description plane: several particular behavioral assays that link low-dimensional measures (sometimes qualitative) to higher level concepts. The promise stems from twenty first century big data technology: a denser and wider sampling of the dimensionality axis, as well as a more systematic exploration, standardization and sharing of conditions along the constraints-dimensionality plane. The challenge is to use carefully designed experiments and theoretical frameworks to project quantitative, contextual and low-level, high-dimensional measurements into high-level, universal and comprehensive explanations of animal behavior: a journey from data to meaning.

and actuators (food and water dispensers) to create complex environments in which data can be collected over days and genetic manipulations studied, which, together with video analyses, can reveal presymptomatic behavioral deviations in mouse models of disease[22]. Yet the more recent development of far less expensive hardware (for example, Arduino microcontrollers) and open software is a potential game-changer.

Behavior evolved in natural environments. Thus, laboratory experiments can sample a greatly reduced subset of behaviorally relevant environments. Efforts to export quantitative methods to more ecological situations are also taking advantage of advances in technology, opening up many new possibilities for monitoring freely behaving animals in wild or semi-wild conditions over large spatial and temporal scales. Fruitful directions include image-based tracking[23], animal-attached remote sensing (for example, using RFID tags[21]), autonomous recording tags, animal-mounted video cameras, and, specifically for terrestrial animals, biotelemetry of physiology as well as location and fingerprints for phenotype recognition and profiling of behavior of individuals and species. Furthermore, the same methods are often also applicable to social interactions that involve more than one animal.

On the whole and regardless of the setting, BBD essentially implies an ability to collect and manage large volumes of data both in density and in extension within the behavioral space (**Fig. 1**). In a weak sense, BBD indicates more precision, more resolution, longer observations, higher number of animals, and data sets across a larger variety of tasks and conditions. In a strong sense, BBD suggests the possibility of fully mapping the behavioral space and of the so-called ethome (in analogy with the genome or connectome). However, to fulfill the promises, how exactly are we to maximize these advantages to really make BBD a game-changer? What are the implications of BBD for the design of behavioral assays and for possible reconceptualization of behavior itself?

The challenge: from more to better

It is clear that we have the capacity to acquire BBD, but the main challenges lie ahead and call for the application of conceptual frameworks to resolve many important issues that are not addressed by data recording alone.

Open data. The potential of BBD is hindered (similar to that of money) when it accumulates, but does not flow. We should find incentives to encourage the habit of data sharing, although this issue is not without complexities (**Box 2**).

From datum to factum. A ballpark estimate of the dimensionality of the raw data from a 'manual' ethogram by a human observer at say 100 bit per s when contrasted with a reasonable video recording yields an astonishing 10,000,000-fold increase in the data rate. The manual pre-video scoring takes the raw data on the observer's retina and converts it into much higher level abstract concepts (for example, the rat froze). What is being described is not merely lower dimensional, it is also higher level. The video camera captures data, but it is not meaningful until it is processed and its dimensionality reduced. Thus, it is clear that prediction and understanding require more than data collection; they require synthesis and conversion of data to meaning (facts, ideas and principles).

Whither natural units. To reduce the dimensionality of the data while moving from lower level to higher level descriptions requires using, creatively and insightfully, constraints that are implied by the choice of behavioral context or assays and analysis techniques. In other big data projects, the units to be measured and the conceptual framework to structure and analyze the data were established a priori. For genomic data, it was known that one ultimately needed to read strings of nucleotides (unless our framework is epigenetics); for electrophysiological data, we know we need to extract spike times (unless our framework gives emphasis to local field potentials); and for a connectome, all synaptic partners must be identified (unless our framework relies on knowledge of synaptic strength).

Difficulty of time segmentation. Because behavior unfolds in time, 'segmenting' or 'parsing' it into discrete chunks is a common

Box 2 Open data: options and imperatives

The problem of behavior is difficult, and the more people willing to tackle it, the better. It is now feasible to share raw behavioral data, yet we lack accepted standards to efficiently and productively do so. Moreover, a shift in our scientific culture seems to be required to incentivize scientists and to evaluate and prune the quality of the data so that intellectual pride and distrust can be transformed into the intellectual joy of sharing and true collaborative spirit. Should experimenters be compelled to record, store and share their raw behavioral data, just as they are being compelled to share, for example, genomic data? Should data be shared on request or simply be open by default? These issues are relevant when it comes to 'small data', and become especially relevant when it comes to big data.

Cons. Collecting data is not equivalent to doing experiments. Experiments require well-conceived designs that probe particular aspects of behavior. Simply generating and sharing large data sets risks diluting such efforts. In addition, storage and sharing is becoming cheaper, but it is still not negligible. Moreover, when each laboratory has its own particular assays and conditions, making comparisons is difficult even if the data is openly available. Replication and reproducibility are not to be taken for granted. The resulting confusion could impede collective progress.

Pros. Collecting, storing and sharing primary behavioral data would allow researchers to revisit it, even much later, in search of (or in light of) new insights. Along with open access publishing and shared analysis tools (for example, open software), open data has many advantages: it can facilitate comparison of data across laboratories, optimize resources, speed up progress, improve research quality, and catalyze a scientific culture of trust, appreciation and collaboration.

Suggestions. Data sharing standards will only arise in an environment that requires them. It should be acceptable to request and access primary behavioral data from the source laboratory. It does not yet need to be required to make all raw data available, as the challenges of such a mandate might overwhelm the more pressing need for innovation. Researchers who manage (and are willing) to both acquire and share such data should not only be encouraged, but rewarded. We ought to overcome our habits, try different solutions to these problems, identify what works and facilitate its adaptation. To lead by example might be the first step: action is more powerful than eloquence.

(although often arbitrary) step in both psychological and ethological approaches. But segmenting behavior will be conceptually challenging if temporal organization is hierarchical or multi-scale. For example, one can differentiate and classify locomotion episodes and grooming episodes, but given that both are rhythmic behaviors, one could further segment each step or grooming cycle as smaller repeated elements.

Poverty of environmental stimuli and affordances. As we have discussed, behavior happens in, and because of, the environment. BBD recording and analysis may bring behavior into view, as a telescope makes visible a universe that is not visible to the naked eye. But unlike for the astronomer peering into the night sky, without providing equally rich stimuli and affordances in the environment, even the most detailed video recording and analysis can only capture a tiny fraction of an animal's ethome. This point is illustrated by sensory neuroscience studies, which explore 'stimulus space' to probe the dependence of an animal's simple binary responses on the environment. How do we even know what the relevant stimulus space is? The problem is even more acute for the side of action itself, which lies in a physical world that is only sparsely computer controllable. For example, there is no current substitute for an encounter with a conspecific or predator.

Limits of control. Compared with our ability to record what is being emitted, our ability to strictly control those variables remains vastly limited: we can constrain, but not strictly limit, the expression of behavior. This problem can be compared with that faced in multi-neuron data, where, despite advances in optogenetics, our ability to record (in terms of numbers and temporal precision) still vastly outstrips our ability to control. One could contrast this with molecular biology, in which progress has depended not on the ability to measure, but on the ability to write (cut, paste, construct), genetic information in the relevant space.

The conundrum of standardization. Although standardization and automation are fundamental to the collection of BBD, they present an awkward dilemma. The brain evolved to control behavior in a complex, rich and non-stationary environment, and many of its most remarkable functions are those related to its ability to adapt to these diverse demands and changing conditions. If our efforts to produce BBD result (or require) avoiding complexity in the experimental environments of our assays, then it is unclear if this data will ever be able to inform our understanding of the brain's most impressive capacities.

The scientist is absent. A paradox related to the automation of BBD is that it induces the scientist to be even less present: we can generate terabytes of mouse data without ever having spent 5 min observing the phenomenon. The insights of ethologists came from their being present for the phenomenon.

Lack of a general framework. To address these challenges, we will need to rely on conceptual frameworks that determine what features of behavior are meaningful, from the myriad features that might be discerned in video. For example, classical learning theory from psychology does not make strong predictions about the details of the articulation of the arm when pressing a lever. Other frameworks, such as optimal control theory combined with biomechanics, do make predictions about the articulation of the arm and required joint torques, yet can predict little about arm behavior in a food-foraging task. The lack of a consensus framework means there is no universal solution for 'writing down' behavior while accounting for its dimensionality. The absence of a universal language is concerning.

As we have seen from the legacy of psychological and ethological approaches, there is a tension between relatively constrained and unconstrained approaches. Below, we examine the effect of BBD on these two different approaches: on the one hand, decision-making and reinforcement learning, which is closely aligned and inspired by classical psychological approaches, and on the other hand, modern ethology and state space analysis, which is more closely aligned with ethology approaches to innate behaviors.

Opportunities in the framework of decision-making

We use the term decision-making to refer to two closely related approaches. The first is perceptual decision-making or psychophysics, a classical approach to quantitatively linking physical characteristics of stimuli with their perceptual effect[24] that has been used in rodents to characterize perceptual and cognitive processes[25,26]. The second is reinforcement learning, an approach mainly concerned with learning how to act in a given situation to maximize reward or value[27]. As perceptual thresholds and sensitivities are measured in psychophysics, state value functions are inferred from patterns of choices, with more frequent choices reflecting states or actions of greater value[28]. Both build on classical psychological work on reinforcer-driven learning (rewards and punishments) to guide behavior, allowing the experimenter to isolate, exaggerate, manipulate and systematically explore behavioral functions.

Scaling up. An obvious benefit of BBD arises naturally from scaling up of the size of the data set. Decision-making tasks in rodents are much more powerful when they include the ability to collect hundreds to thousands of trials in a single session or to amass tens or even hundreds of thousands of trials from a given animal or a behavioral data set. The ability to apply relatively high-throughput automated (live-in cage)[21] or semi-automated behavioral assays[29] can greatly aid in reaching these levels of trials. Such a large corpus of data may reveal aspects of behavior that are small, but lawful, and those that may require conditioning on many different variables (that is, dividing the data set among many conditions). This is particularly important in analyzing the effects of learning in past trials on the performance of a given trial[30], as the number of conditions to be included increases exponentially with each past trial. Thus, large data sets may reveal stimulus/choice history effects that would otherwise have been simply choice variability.

From discrete to continuous measures. The core unit of many psychological assays is the trial, which implies a temporal segmentation assumption. Trials are composed of several different phases in a sequential chain. For example, a trial might begin with a criterion of the animal signaling its readiness and then proceed from stimulus presentation to response to outcome. An experimental session typically includes rules about how longer sequences of trials are structured (for example, different types of stimuli randomized or clustered in blocks). BBD approaches can benefit decision-making studies by expanding the dimensionality of the measurements being made. Although most of these approaches have thus far relied mainly on minimal binary response measures (for example, lever up, lever down; infrared beam breaks with the snout), the magnitude of internal perceptual or cognitive variables are likely to be continuously valued and evolving in time. Given that, in neural terms, motor systems are not fully insulated or isolated from the cognitive systems, information about the time course of unfolding decisions may be found in continuously expressed behavior such as the micro-movements of the head[31,32].

Noticing the unconstrained. In decision-making approaches, it is traditional to constrain the available behavioral outputs as tightly as possible. Rodents may indicate choice through the selection of a particular physical path while moving through a maze[33], one of a number of available nose ports[17,20,25,34] or levers, by positioning a manipulandum, or licking at particular reward delivery tubes. If we ensure that we avoid confounds, BBD can reveal the 'unconstrained' as a rich source of insight rather than a nuisance. Decision-making studies principally reinforce and measure binary choice output, but response times, when unconstrained, are extremely revealing about the behavior[35]. For example, response times to obtain outcomes reveal expected value[36], allowing one to measure value on a trial-by-trial rather than average basis, and the waiting time of an animal for a delayed reward indexes confidence in the preceding perceptual decision[26]. In a similar manner, the application of high-speed video data is likely to provide key insights into the dynamics of less-constrained movements executed in the course of meeting task demands[34].

Virtual and augmented reality. Computers have already made exploring stimulus space a relatively tractable problem, at least in the visual and auditory domains, whereas somatosensory, vestibular, olfactory and other domains remain much more challenging. When considering the experimental subject not only as being acted on, but acting on the world, the issue is also challenging for computers. A very interesting opportunity for BBD in the psychological framework is that, after acquiring a rich measure of behavior (i.e., video), it will also be powerful to define, 'virtually', quantitative readouts. For example, in the classic operant conditioning lever-press task, a more flexible reporter could be implemented using a video-based real-time feedback control system. Approaches such as this have already been implemented with respect to location in locomotor behavior[37], which is undoubtedly an ethologically important domain for rodents. To provide richer opportunities, even more complex readouts can be harnessed to give feedback to the animal, providing virtual affordances (for example, rearing events could be detected and linked to a reward or another stimulus). This approach could also provide a natural connection to more ethological descriptions of behavior.

Computational models. The use of computational models can provide a powerful mathematical description of the features of behavior. These models comprise higher level descriptions of behavior by which raw behavioral data is transformed from a lower level and higher dimensional representation by inferring the dynamics of a smaller number of state variables. Three examples are integrated evidence in models of bounded accumulation of evidence[31], experienced value in models of reward-based decisions[38] and subjective confidence in models of higher order decision-making[39]. Critically, these models serve as the scaffold by which the results obtained from a specifically constrained behavioral assay can be generalized to other assays and environments. More detailed models instantiate abstract concepts and theories in a way that allows them to be cached out into observables. Notably, in addition to providing concise and predictive models of behavior, these models also constitute linking hypotheses through which behavioral and neural data can be related[40].

Opportunities in the framework of ethology

Ethology, the study of animal behavior under natural conditions, relied on extensive observation and annotation of behavioral states and events by human observers. Particular attention was often paid to the phylogenetic history of the species being studied and the selective pressures applied to organisms by their natural and social environments. The legacy of modern neuroethology, specifically when compared with the psychological approach, provides less constrained experiments: rather than placing constraints in the environment and creating special places by building levers and pokes, ethologists let animals express their behavior more freely at the expense of control.

Making ethograms reversible. The annotations of expert ethologists grasped meaningful behavioral states by segmenting the continuous flow of behavior into a sequence of discrete categories sewn together by transitions between those states in an ethogram representation. Segmentation embodies the theory in the observation[41]. And this is irreversible: there is no possible return into the underlying phenomena. Computer-based approaches transform the ethological approach because data acquisition is no longer inextricable from data analysis. Now, with BBD, continuous high-resolution multidimensional streams of raw data can be collected, saved and shared, providing the opportunity to revisit them as many times as necessary without getting stuck in *ad hoc* behavioral categories and summary statistics. Data can be reanalyzed by the same or different laboratories. Data can also be collected and stored just in case, allowing inspection in later stages of an experiment.

Scaling up in effort and timescales. Ethological approaches rely on behavioral classification or annotation to identify features of interest and quantify their occurrences and relationships. BBD provide the opportunity to automate this old procedure with the use of computer algorithms. The process can be supervised (aided by the judgments of trained observers), with scientists directly translating their subjective expertise into an algorithm, which then prescribes the processing of the data[42]. It can also be unsupervised (relying on features of the data itself for classification) and, in principle, less biased[43]. Automated annotation allows fixed rules to govern segmentation of behavior over large amounts of data, providing standardization. It is also vastly faster, greatly expanding the scale of what can be annotated. This opens the opportunity to study the behavior of individuals on very short and very long timescales that were previously inaccessible to unaided observers[44]. From ultra-fast maneuvers during prey capture[45] to non-rapid behavioral assays in naturalistic conditions[46], BBD can provide a window into entirely new phenomena.

Finding simplicity in higher dimensions. BBD makes it possible to densely sample the many degrees of freedom of a behavioral process. Although segmentation and ethograms are one way to look for simplicity in higher dimensions, other conceptual frameworks operate on high-dimensional continuous data itself (such as information theory[47,48]), lessening 'the fallacy of misplaced concreteness'. For instance, applying statistical mechanics formalism, the collective behavior of flocks of birds, measured through continuous correlations in the location and velocity across neighbors, is shown to be posed at criticality[49]. Beyond the ethogram representation, BBD allows us to densely estimate the distance between distributions of continuous kinematic variables[50], the covariance matrix of body postures[51], times series motifs and grammars[52,53], or low dimensional embeddings naturally emerging from spatiotemporal patterns in pixel space[54], thereby mapping the phenotypic space[55].

Contrasting contexts: sampling, quantifying and recreating the Umwelt. A fundamental mission of the ethological approach is to integrate the study of the animal behavior with its world or 'Umwelt'[56]. Thus, thoroughly characterizing an animal's natural behavior generally requires observation across different environmental conditions. BBD approaches will facilitate this by both enabling larger scale studies and opening new possibilities such as monitoring and controlling the sensory input as an animal negotiates its world (estimating the temporal dynamics of olfactory input as it orients in chemical gradients[57]). Exploring behaviors across natural environments from the animal's perspective is very revealing[58]. One can examine the relationship between sets of different behaviors to determine which are invariantly associated versus those that are merely coincidental[59]. Similarly, cross-environment comparisons will help to distinguish circumstantial from essential neural-behavioral correlations[60,61]. Finally, contrasting apparently similar behaviors in different environments can also reveal different causes of apparently identical behaviors. For example, the difference between habitual and goal-directed lever pressing can be distinguished by environmental manipulations such as sensory-specific satiation and contingency degradation. Thus, environmental manipulations help us understand why a certain behavior is being performed, revealing alternative neural substrates for the same action[62].

De-aggregating variability. BBD will greatly increase not only the size and richness of data sets from each individual, but will bring the number of animals tested in the same assays into the hundreds or even thousands, as has been achieved with insects[63]. This combination will allow behavioral descriptions that go from average species behavior to individual behavior. This will allow neuroscience to address the important question of animal personality or individuality from a neuroethological perspective[64]. At the same time, combined with the willingness to share data (**Box 2**), this combination of rich data from many individuals will greatly enhance the possibility for identifying sources of variability across laboratories, thereby setting higher standards for experimental protocol/assay design and behavioral analyses and achieving less fragmentary and idiosyncratic descriptions[65].

Characterizing spontaneous behavioral processes. The stimulus-response approach to behavior has proven to be as successful as it is convenient, as one can systematically repeat the same external sensory protocol in order to estimate the statistics of animal responses. In the complementary view, in which brains are output-input devices[66], it is much harder to collect the necessary amount of data to discover high-level rules generating the (apparently) noisy behavior[67,68]. BBD will be an important step in expanding ethological investigations to the study of spontaneous behavior, where the animal, rather than the experimenter, calls the shots. Conceiving behavior as a continuous process (a wave rather than particles), behavioral transitions can emerge as difference and repetition captured via recurrences of the dynamical system[69]. From actions never previously performed[70] to the origins of creativity[71], BBD might allow us to collect enough evidence to understand the evolution of behavior, a long standing goal of ethology[72].

Outlook

The main challenge confronting behavioral science is extracting meaning from an ever-increasing amount of information (**Fig. 1**). Technological advances, despite offering new opportunities, cannot substitute for the development of new experimental designs and improved conceptual frameworks. When faced with the promise of BBD, behavioral science must define its metrics for achievement. Thus, we would extend the discussed opportunities by considering what success might look like for behavioral science in a future era of BBD.

Making sense of neural variability. Recent innovations in imaging and electrophysiology have enabled the collection of increasingly rich descriptions of neural data. However, we risk throwing away as unexplained much of that richness for lack of similarly rich behavioral data. BBD and the toolset of statistical methods necessary to relate that behavioral data to itself will provide new approaches for explaining greater amounts of neural variability, thereby providing richer neural correlates.

Convergence of ethological and psychological approaches. BBD can foster a unification of the ethological and psychological approaches to animal behavior: the convergence of states and trials. For example, 3 years of continuous monitoring of mice burrowing in the wild will allow an experimenter to select from 1,000 instances of forepaw movement and ask questions that were previously circumscribed to the realm of Skinner boxes, all while retaining the essential ethological grounding. Large amounts of data may implicitly contain the conditions necessary to isolate particular behavioral events while controlling for potential confounds, which is indeed the goal of tightly controlled behavioral tasks used in the laboratory.

Homology in ethology. Behavioral science celebrates diversity while seeking for universals, elements of convergence that signal life's phylogenetic and ontogenetic solutions to problems in the physical world[73].

So far we have a poor grasp of what behavioral universals might look like. For example, the claim that 'the rat is rearing' creates a discourse that is based on language labels that are often not applicable to other animals and assumes 'immaculate perception' at the observation stage, which is tainted with certain arbitrariness. Very few studies have succeeded in identifying forms of behavioral invariance and universality across species[74,75], nor do we know whether behavioral units exist at all. When considering anatomy, we use the notion of homology across taxa to substantiate the universality of particular forms. A future behavioral science might complete Lorenz's vision[72] of establishing homology in ethology.

Ethomes, sub-ethomes and ethons. One might proclaim the ethomics era, and imagine its product to be an ethome, a complete description of the set of behaviors manifested by a species in its natural environment. Considering that behavior in a full sense includes complexities such as language and tool use, it is clear that a complete description is impossible for the human species. Even for rodents, as we have argued, behaviors must be considered in the context of an environment: conceptually, there is no behavior in a vacuum. Certainly, exploring more expansive and previously inaccessible regions of the behavioral space may be possible and informative, and sub-ethomes would make sense as descriptions of behavior restricted to a particular environment. Nevertheless, an exhaustive, but contingent, description is not the goal. Rather, we argue that the biggest service of BBD would be to promote the development of new unifying frameworks for animal behavior. This may even lead to the identification of fundamental behavioral units (let us call them ethons), from which organizing principles and postulates, as occurred for genes, genetics and genomics, might revolutionize the field.

On the whole, the success of BBD will foster the end of its utility: we will then know what degrees of freedom to look for, how, where and why. Reaching these goals places implicit, but inexorable, constraints on the way we do science: it requires considerable effort to explore and adopt better ways of standardizing data so that it can be reused and compared and a collaborative relationship with our peers, with an open attitude to share our data and to appreciate theirs. Ultimately, it will act to renew our habits and become willing to make one more step into the unknown, where new science can take place.

COMPETING FINANCIAL INTERESTS
The authors declare no competing financial interests.

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