Big Behavioral Data:
Psychology, Ethology and the Foundations of Neuroscience

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Abstract

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 impact of accelerating advances in technology for behavioral studies, focusing on rodents as an exemplar. We frame our perspective in three dimensions: 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 20th 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 novel theoretical frameworks and improved experimental designs matches the technological progress.

1. Introduction: Behavior is foundational

Behavior is "what animals do". It can be defined as the muscular output of an organism or, alternatively, 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. Therefore, 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 (e.g. 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 where 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 and psychology, and the social sciences converge.

The study of behavior has a long and rich history that we must try to summarize in order 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 19th and 20th 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 based on their consequences[8,9], 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 axis), the main promise of BBD (dimensionality axis) and the challenges faced in applying it (description axis). We can see (and will argue) that (1) the issue of constraints is an old conceptual struggle still unresolved, (2) moving to higher levels of description while reducing dimensionality remains a universal scientific motive, but one that is also dangerous when premature, and (3) technology delivering BBD has enlarged the “playing field” in ways that interact with (1) and (2).

The primary aim of this manuscript 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 will do so through the primary lens of rodent behavioral studies, whilst bringing comparisons to other species and other "omics" when useful, stressing the implications for the interpretation of neural data. We first (Section 2) review the tools and technology that are contributing to BBD and the promise for behavioral studies that they represent. We then (Section 3) discuss the challenges inherent in applying those tools in a scientifically productive manner. In the following two sections (Sections 4 & 5), we offer 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 (Section 6) with our view of the longer-term impact of BBD for the future of neuroscience.

2. The promise: Advancements 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 offered access to new spatial and temporal scales that were 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 (mm resolution), at VGA resolution, day and night (IR 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 (EMG), 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-lab reproducibility, once committed to a given set of constraints implied by a uniformized behavioral setup. These approaches have already seen substantial application in smaller species, and have proven valuable for rodent studies as well[19]. Automation has been deployed on two levels. First, reducing the need for human monitoring and intervention, even done remotely or offline[20]. These systems still require manual transfer of animals into and out of cages, etc. Second, "live-in" systems where rodents live in the behavioral assay or shuttle between "home cage" and assay by themselves[21]. Commercial systems have integrated RFID technology with sensors and actuators (food and water dispensers) to create complex environments where data can be collected over days and genetic manipulations studied which, together with video analyses, can reveal pre-symptomatic behavioral deviations in mouse models of disease[22]. Yet the more recent development of far less expensive hardware (e.g., 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 (e.g., using RFIDs[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 that ability to collect and manage large volumes of data both in density and in extension within the behavioral space (see **Figure 1** for details). In a weak sense, BBD means more precision, more resolution, longer observations, higher number of animals, and datasets across a larger variety of tasks and conditions. In a strong sense, BBD suggests the possibility of "fully mapping" the behavioral space, and thus it suggests the possibility of the so-called "ethome" (in analogy with the genome or connectome). We will return to this issue in Section 6.

However, to fulfill the promises, how exactly are we to use these advantages to the maximum 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?

3. 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. Consider among these:

Open data. The potential of BBD is hindered (like 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 (see **Box 2**). We do not have space to unfold this here.

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/s, when contrasted with a reasonable video recording, yields an astonishing 10-million fold increase in data rate. The "manual" pre-video scoring has taken the "raw data" on the observer's retina and converted it into much higher-level abstract concepts (e.g., "the rat froze"). What is being recorded 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. So, 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 whilst 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); 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 (though 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 since 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 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 by exploring "stimulus space" probes 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, nothing yet will substitute for an encounter with a conspecific or predator.

Limits of control. Compared to 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 to 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 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 five minutes observing the phenomenon. The insights of ethologists came from their presence to 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. Next, we will examine the impact of BBD on these two different approaches: first (Section 4) "decision-making and reinforcement learning", which is closely aligned and inspired by classical psychological approaches and second (Section 5) "modern ethology and state space analysis", more closely aligned with ethology approaches to innate behaviors.

4. 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 impact[24] that has been used in rodents to characterize perceptual and cognitive processes[25,26]. The second is reinforcement learning (RL), an approach mainly concerned with learning how to act in a given situation in order 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. This methodology facilitates a mechanistic understanding in which the parts of systems are isolated and manipulated.

Opportunity 1: 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 100's to 1000's of trials in a single session or to amass 10's or even 100's 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 (i.e. dividing the data set amongst many conditions). This is particularly important in analyzing the effects of learning in past trials on the performance of a given trial[30], because 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.

Opportunity 2: 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 (e.g., 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. While thus far most of these approaches have relied mainly on minimal binary response measures (e.g., 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. Because 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 micromovements of the head[31,32].

Opportunity 3: 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 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. So, ensuring we avoid confounds, BBD can reveal the "unconstrained" as a rich source of insight rather than a nuisance. Consider that 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 add key additional insights for the dynamics of less constrained movements executed in the course of meeting task demands[34].

Opportunity 4: Virtual and augmented reality. Computers have already made exploring stimulus space a relatively tractable problem, at least in the visual and auditory domains, while somatosensory, vestibular and 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, once 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 paradigm, a more flexible reporter could be implemented using a video-based real-time feedback control system. Approaches like 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" (e.g., 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.

Opportunity 5: 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/theories in a way that allows them to be cached out into observables. Critically, 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].

5. 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 to 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.

Opportunity 1: 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, thus 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.

Opportunity 2: 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), where scientists directly translate 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 thus 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, therefore greatly expanding the scale of what can be annotated. This opens the opportunity to study the behavior of individuals at very short and very long time scales 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.

Opportunity 3: Finding simplicity in higher-dimensions. BBD makes it possible to densely sample the many degrees of freedom of a behavioral process. While 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 the 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 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], thus mapping the phenotypic space[55].

Opportunity 4: 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 both by enabling larger-scale studies and by 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 vs. 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].

Opportunity 5: De-aggregating variability. BBD will greatly increase not only the size and richness of datasets from each individual, but will bring the number of animals tested in the same assays to 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 (see **Box 2**), this combination of rich data from many individuals will greatly enhance the possibility for identifying sources of variability across laboratories, therefore setting higher standards for experimental protocol/assay design and behavioral analyses and achieving less fragmentary and idiosynchratic descriptions[65].

Opportunity 6: Characterizing spontaneous behavioral processes. The stimulus-response approach to behavior has proven as successful as convenient, since one can systematically repeat the same external sensory protocol in order to estimate the statistics of animal responses. In the complementary view, where 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 a key step to expand 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 performed before[70] to the origins of creativity[71], BBD might allow us to collect enough evidence for understanding the evolution of behavior, a long standing goal of ethology[72].

6. Outlook

The main challenge confronting behavioral science is extracting meaning from ever increasing information (**Figure 1**). Technological advances, despite offering new opportunities, cannot substitute for the development of novel experimental designs and improved conceptual frameworks. When faced with the promise of BBD, behavioral science must define its metrics for achievement. Thus, in closing we would extend the opportunities of previous sections 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 to explaining greater amounts of neural variability, thus 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, three years of continuous monitoring of mice burrowing in the wild will allow an experimenter to select from thousand instances of forepaw movement and ask questions that previously were 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 paradigms 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 "the rat is rearing" creates a discourse that is based on language “labels”, often not applicable to other animals, and assumes “immaculate perception” at the observation stage 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/postulates, as was for genes/genetics/genomics, might revolutionize the field.

On the whole, the success of big behavioral data will foster the end of its utility: we will then know what degrees of freedom to look for, how, where, and why. Reaching these significant 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 demands to renew our habits and be willing to make one more step into the Unknown, where new science can take place.

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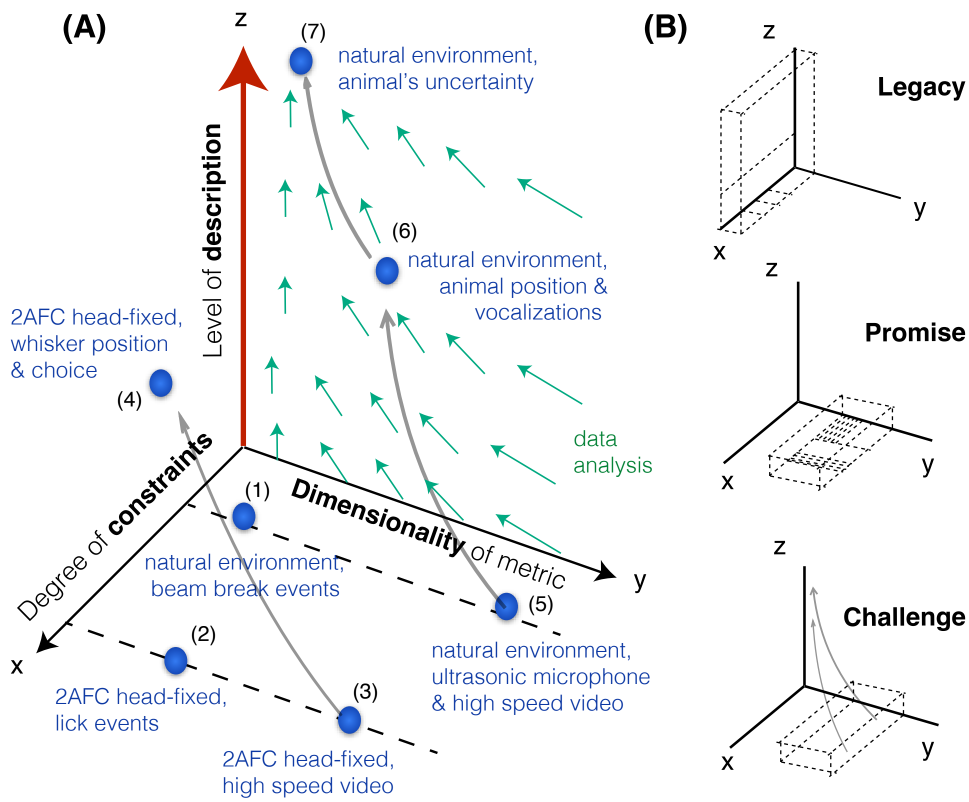

Figure 1. (A) Conceptual representation of three main axes in the behavioral sciences space: experimental design (constraints, x-axis), measurement resolution (dimensionality, y-axis) and abstraction level (description, z-axis). **Constraints:** The degree of constraints is imposed by the experimental context—lower in the case of ethologists, high in the case of the psychologists. Constraints limit the scope of behavior, narrowing the possibilities for expression to a particular set of conditions, at the same time that dictate the affordances available to the animal (e.g. climbing could only be expressed in an environment that affords climbing). Constraints also give a frame of reference, thus they express hypotheses about what is important to observe. A behavioral assay, by standardizing constraints, facilitates comparison and replication of behavior within the same assay, but hinders generalization of the findings to new settings. **Dimensionality:** Classical ethologists and psychologists were both limited to lower dimensional data available by direct observation, note-taking, etc, thus limiting the precision and dimensionality of their records. The development of computer and information technology has opened up new possibilities, offering us more precise, broader and higher dimensional observations. **Description**: the level of description ranges from the complexity of primary data (low level) to abstract metrics and general concepts (high level). One can analogize this to the way neuroscience pictures the brain as moving from primary sensory representations to view invariant object representations. General principles are the goal of the scientific process (and of vision) and this was shared amongst all behavioral schools. At the same time, high-level descriptions can narrow and blind the experimenter to other interpretations (a child drawing a chair reproduces not what hits his retina but his concept of a chair -four legs- being blind to its true form). **Blue dots** serve as different interrelated examples: relaxed constraints on animal behavior in naturalistic conditions recorded at low dimensionality via beam break events (1) can be constrained much further (motion along x-axis) in a 2AFC head-fixed preparations with lick events as measurement (2), whose dimensionality can in turn be increased (motion along y-axis) by acquiring high speed video data (3), from which further analysis (motion along z-axis) can detect whisker position and choice (4). In a more naturalistic assay (5) 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 (6) to, finally, infer the animal's emotional state or its uncertainty about the world (7) in what therefore represents a high level of description. **(B)** We map the activity in the behavioral space along the constraint, dimensionality and description planes to the legacy of psychology and ethology, the promise of big behavioral data, and the current challenges of behavioral neuroscience. The **legacy**, inherited from 20th century ethology and psychology, is schematized in the constraints axis: several particular behavioral assays that link low dimensional measures -sometimes qualitative- to higher level concepts. The **promise**, stemming from 21st 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.

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. While 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, or meditation. Three key attributes of animal behavior are:

(1) 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 significant attempts to grasp such relational aspect of animal behavior.

(2) Behavior is **dynamic**. It is a process where change is both accidental and essential: the animal changes yet it is still the same. As physiology is distinguished from anatomy by dynamics, behavior is manifested through 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, being itself a non-trivial inference. Theories and frameworks to quantify the process of becoming can greatly advance our understanding of time and dynamics in animal behavior.

(3) Behavior is **high-dimensional**. It appears complex and variable (unpredictable). The number of behavioral effectors and their degrees of freedom (e.g. arm or vocal articulation) reduces somewhat 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 (e.g. go left implies not go right), but do not rule out concurrent manifestation of multiple "behaviors" (e.g. talking and walking). Dimensionality reduction techniques are thus decisive in the study of animal behavior.

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 as to find way of incentivizing scientists and evaluating/pruning the quality of the data, so that intellectual pride and distrust can be transformed into intellectual joy of sharing and true collaborative spirit. Ought 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 "upon request" or simply open by default? These issues are relevant in "small data", and become specially relevant in "big data".

(1) **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 datasets risks diluting such efforts. Plus, storage and sharing is becoming cheaper, but it is still not negligible. Moreover, when each lab has their own particular assays and conditions, making comparisons is difficult even if the data is openly available. Replicability and reproducibility are not to be taken for granted. The resulting confusion could impede collective progress.

(2) **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 (e.g. 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.

(3) **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 lab. It need not, yet, 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.