



Review

Beyond simple laboratory studies: Developing sophisticated models to study rich behavior

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Abstract

Psychology and neuroscience are concerned with the study of behavior, of internal cognitive processes, and their neural foundations. However, most laboratory studies use constrained experimental settings that greatly limit the range of behaviors that can be expressed. While focusing on restricted settings ensures methodological control, it risks impoverishing the object of study: by restricting behavior, we might miss key aspects of cognitive and neural functions. In this article, we argue that psychology and neuroscience should increasingly adopt innovative experimental designs, measurement methods, analysis techniques and sophisticated computational models to probe rich, ecologically valid forms of behavior, including social behavior. We discuss the challenges of studying rich forms of behavior as well as the novel opportunities offered by state-of-the-art methodologies and new sensing technologies, and we highlight the importance of developing sophisticated formal models. We exemplify our arguments by reviewing some recent streams of research in psychology, neuroscience and other fields (e.g., sports analytics, ethology and robotics) that have addressed rich forms of behavior in a model-based manner. We hope that these “success cases” will encourage psychologists and neuroscientists to extend their toolbox of techniques with sophisticated behavioral models – and to use them to study rich forms of behavior as well as the cognitive and neural processes that they engage.

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1. Introduction

The dominant approach in cognitive psychology and neuroscience involves manipulating task instructions and stimuli to study their effects on internal cognitive processes, such as perception, attention, memory or decision-making. Most laboratory studies use simple forms of behavior, such as button presses, as a way to probe internal cognitive processing; for example, by looking at reaction times with different sets of stimuli, like words or shapes, to establish which ones require more processing. These laboratory studies therefore do not elicit “behavior” in all of its richness, but rather basic “behavioral responses” to experimental manipulations. One reason why experimenters find it useful to restrict (if not inhibit) the behavior of humans and other animals is that it can be highly variable if not constrained in some way, hence rendering its interpretation more challenging. In classical psychology, neuroscience and cognitive science, this challenge is traditionally approached by tailoring experimental designs whereby behavioral variability, considered a confounding factor irrelevant to the object of study (e.g., a potential cause of “movement artifacts” in neuroimaging), has been attentively restricted. Experimental tasks in the laboratory have therefore been mostly detached from human daily life experience, thus removing most of the variability and complexity that intrinsically shape behavior in ecologically valid settings [1–3].

On the other hand, the study of less constrained, richer forms of behavior grants the possibility of addressing new questions and new problems in psychology and neuroscience. Here, we use the term “rich behavior” to denote behaviors that humans and other animals typically exhibit in ecologically valid conditions, such as when foraging for food or shopping, playing sports or videogames, or finding their way through a crowded town. These and other examples of rich, naturalistic behavior imply a synergy between various perceptual, motor, and cognitive functions - for example, attention, perception, goal-seeking, navigation, memory, and others [4,5] - rather than recruiting them in isolation, as is commonly done in laboratory studies. Furthermore, naturalistic behavior often engages sets of inter-dependent processes that may unfold over different time scales. For example, soccer players have to acquire information about the state of the game while running and deciding where to position themselves, or whether to pass or shoot the ball. Similarly, a car driver has to monitor the road and the movements of the other cars while continuously making decisions about where to turn, whether to accelerate or stop the car, etc. Similar forms of behavior are difficult to fit in the classical structure of laboratory studies, which benefit from measuring activity across repetitions of similar discrete “trials” and controlled manipulations of stimuli in “blocks”. For example, when studying how a car driver enters a new lane, it is not straightforward to define when the “trial” starts or the time of “stimulus onset”, since the action under study (entering a lane) is embedded in a continuous ongoing activity of “car driving” [6,7]. Other challenges include the difficulty of characterizing the high inter- and intra- individual variability of behavior that might emerge in ecologically valid conditions and the necessity of disentangling causes and consequences within a convoluted network of interactions between multiple agents and the environment. All of this makes the study of rich behavior particularly challenging - but also potentially very rewarding for psychology and neuroscience, as it could complement the traditional (reductionist) laboratory-based approaches to study cognitive functions [1]. Although the full complexity of natural behavior can be overwhelming, the last decade has seen promising advances in this direction where sophisticated experimental procedures and analysis methods have been developed and begun to mature.

The study of rich behavior in humans and other animals is nowadays largely confined to a few fields that are not well integrated with mainstream psychology and neuroscience (with some exceptions, see below) [8]. One such field is motor control, which mostly studies how behavior is organized outside its relations with internal cognitive processing. As David Rosenbaum remarked in 2005, it tends to be treated as “the Cinderella of psychology” [9], i.e. it is neglected in most textbooks. Another field is the study of joint actions and the behavior of multiple people pursuing cooperative (or competitive) goals [10]. Such social interactions often elicit quite rich forms of behavior, such as when people jointly grasp objects [11], lift objects from each other’s trays [12], walk together [13], engage in a complementary collision/avoidance interaction [14], or coordinate during a music ensemble performance [15]. Even so, most studies tend to confine the variability of such behavior to ease their analysis. Yet another field is ethology, which has long studied rich behavioral patterns in animals in the wild (and more rarely in humans [16]) and has developed various methods to formalize them, such as ethograms [17] and automated methods for a quantitative characterization of behavior that may support studying the link between brain and behavior [18]. However, ethology proceeds largely independently from psychology and neuroscience, despite the alignment of interests between these domains [19]. Other fields, such as sports analytics, artificial intelligence, and robotics, are interested in behavior for reasons that

are often independent from, but interestingly aligned with, those driving research in psychology, neuroscience and cognitive science.

Interestingly, all these fields (and others) are developing useful analytic techniques and computational models to study rich forms of behavior, and these can be extremely useful for psychology and neuroscience [20]. In other words, there are novel opportunities offered from state-of-the-art methodologies and technologies in diverse research fields to broaden the range of tools that psychology and neuroscience typically use, and which permit meeting at least some of the challenges of studying rich forms of behavior, including social interactive tasks. These methods and techniques include everything from clever experimental designs to efficient recording techniques to powerful statistical and analytical tools. However, we argue that the development of sophisticated computational and theoretical models of behavior is of particular importance.

By “sophisticated models” we are not referring to models that are (necessarily) complex from a computational perspective, but rather those that are able to formalize “rich” aspects of naturalistic behavior: foraging, approach, escape, and team sports are just a few examples. As highlighted above, rich behaviors are characterized by a variety of movements, cognitive and neural processes that cannot be easily addressed by mainstream computational models in psychology and neuroscience, which are typically designed to deal with one or a few kinds of cognitive processes and movements (e.g., button presses after stimulus presentations as in psychophysics experiments). On the contrary, the sophisticated models that we envisage - and of which we will provide some examples below - should include internal variables able to capture this cognitive and neural richness, which could be used for hypothesis-driven analyses of behavioral and neural data.

In a similar way, the study of “rich behavior” does not necessarily need to address naturalistic behavior in the wild. A thoughtful trade-off between seeking naturalistic behavior and guaranteeing experimental control is indeed crucial to rigorous scientific investigation. Tasks with increasing degrees of complexity should be considered as they can bring new insights into the complex interplay between perception, cognition, and motor behavior; in turn, this will allow researchers to address unconstrained forms of behavior in a progressive fashion. A clear example comes from the introduction of mouse tracking as an alternative for button press in decision-making studies. The kinematics of trajectories reaching the chosen target has been shown to bring along rich information about critical factors in decision making processes, such as uncertainty, changes of mind, and their interplay with motor control mechanisms [21,22].

There is clearly a bidirectional link between the study of rich behavior and the development of sophisticated computational models. While an interest in understanding and predicting rich behavior could stimulate the design of sophisticated computational models (or their adaptation from other fields), so too might such models guide or expand the development of more innovative experimental designs and help interpret the complex experimental data that they make available. Similarly, there is a tight interplay between the availability of large datasets and the development of new computational methods. This finds a prime example in sport analytics whereby the challenges posed by predictive analytics based on massive multidimensional data call for new developments integrating methods such as game theory, computer vision and statistical learning [23].

In the rest of this article, we first summarize some benefits of studying rich and ecologically valid forms of behavior to advance psychology and neuroscience. Then, we discuss some challenges of studying rich behavior and explain what is needed to make its study feasible and rigorous through the development of sophisticated computational models. We next illustrate some “success stories” in psychology, neuroscience and other fields (sports analytics, ethology and robotics) that have fruitfully addressed rich forms of behavior and (in most cases) used sophisticated computational models for this purpose. Finally, we conclude with a distillation of our proposal and provide a short list of recommendations for psychology and neuroscience researchers interested in developing sophisticated models to study rich behavior.

2. Why study rich and ecologically valid behavior

Most laboratory studies to date seek controlled and replicable experimental designs and setups, by greatly restricting the behavior of participants. While this approach has several merits, it comes at the risk of restricting the object of analysis to artificial contexts that do not generalize well to real-world conditions. The study of rich forms of behavior is important to advance research in psychology and neuroscience for at least five reasons.

First, measuring rich behavior provides a unique window into cognitive processes in ways that provide broader insights than the usual laboratory studies. This is because bodily movements broadly constructed (e.g., reaching move-

ments, postural adjustments, facial movements) as well as interoceptive signals (e.g., cardiac signals) offer invaluable indexes and measures of underlying cognitive and affective states, as well as dynamics of attention and motivation. Using simple kinematic measures of eye, finger, computer mouse or full body movements during decision-making has permitted access to rich indexes of decision uncertainty [21,22,24], changes of mind [25–27], confidence [28], and motivation [29,30], beyond the usual measures like accuracy and reaction times that are typically used in psychology and neuroscience. Interestingly, such continuous measures of decision-making may allow inspecting the underlying information and control processes at both the continuous [31] and the discrete [32] level.

To exemplify the extent to which motor behavior may bring a rich trace of mental activity, Fig. 1 shows the finger movements of a participant during a problem-solving task that resembles the “traveling salesman” problem [33]. The task consists of starting from the yellow node and finding a path that connects all the red nodes, without passing through the same node twice. Fig. 1a-i shows the time course of the finger movements (in blue) and of the selected path (highlighted in gray) during the task. The density of the blue circles that form the finger trajectory illustrates the finger velocity, which is slower / faster when the density is greater / smaller. Initially, the player moves fast up and then right (Fig. 1a-b) but then rapidly “changes her mind” twice: she goes backward and then forward again (Fig. 1c) until she reaches the next node and pauses (Fig. 1d). After the short pause, she moves to the right and then down (Fig. 1e) but then “backtracks” by moving upward (Fig. 1f). The last three panels show that afterwards, the player completes the problem, by making one pause at the bottom-right node (Fig. 1h) and then moving towards the final red nodes without further changes of mind - and with a rapid acceleration near the end (Fig. 1i). This example illustrates the richness of kinematic data that can be obtained by tracking continuous movements during a cognitive task. As highlighted above, kinematic data such as movement direction and velocity, pauses and changes of direction can provide important cues about cognitive variables which would not be accessible by simple response time measurements: for example, decision confidence could be plausibly related to speed, while uncertainty and changes of mind could be plausibly related to pauses and changes of movement direction.

Measuring movement kinematics during reaching and grasping actions also permits accurate decoding of motor intentions, such as the intention to grasp a bottle to drink or to pour [34], and communicative intentions, such as the intention to illustrate the task objective to a co-actor [35]. Measuring movement kinematics during joint action permits unveiling “sensorimotor” forms of communication – such as the subtle motor adjustments people make to render their intentions more legible by their co-actors during cooperative tasks, or conversely to hide their intentions during competitive tasks (e.g., a soccer player who “feints” an opponent) – and which provide experimental access to hidden cognitive variables, like helping or hindering goals [36]. Outside the laboratory, recordings of team positions and movements during sports provide an excellent novel perspective on individual decision-making styles and team tactics [37,38]. These are just some examples demonstrating the value of being able to elicit, measure and analyze rich behavioral patterns for researchers who are interested in cognitive processing rather than action per se.

Second, designing experiments that allow for rich forms of behavior rather than just simple responses to stimuli helps overcome a reductionist bias in psychology and neuroscience [39]. It is common in these domains to use a “divide-and-conquer” strategy to study cognitive phenomena (e.g., how people make perceptual decisions or how many items they remember) in isolation, by devising designs that try to elicit only one cognitive process at a time, while eliminating the interdependencies between them in the real world [40]. Despite the pragmatic benefits and numerous successes of this method, it is becoming increasingly clear that cognitive and neural processing cannot be fully understood in a piecemeal manner and the distinctions that we draw in psychology and neuroscience between cognitive abilities (e.g., attention, memory and planning) reflect outdated taxonomies that are not grounded in brain structure and function [41,42]. Naturalistic behavior epitomizes instead the full richness and interconnectedness of cognitive processing. For example, deciding to whom to pass the ball during a soccer match implies a synergy between what we usually call attention, perception, decision-making, memory, prediction, motor skill and much more. Given that addressing these synergies is methodologically challenging, most psychologists and neuroscientists stay away from sophisticated behavior. However, we should not confound our methodological difficulties with the goals of our disciplines: psychology and neuroscience are ultimately interested in how the brain orchestrates a plethora of cognitive processes to steer adaptive action, not – or not only – in how each cognitive function or brain network works in isolation. Developing models to analyze and reproduce sophisticated behavior can help us make progress towards understanding the full range of adaptive cognitive and brain mechanisms - or “the whole iguana” [43].

Third, studying rich behavior is fundamental to understanding the brain in the context in which it evolved [44–47]. The whole purpose of having a brain in the first place is steering rich, adaptive behavior in the real environment

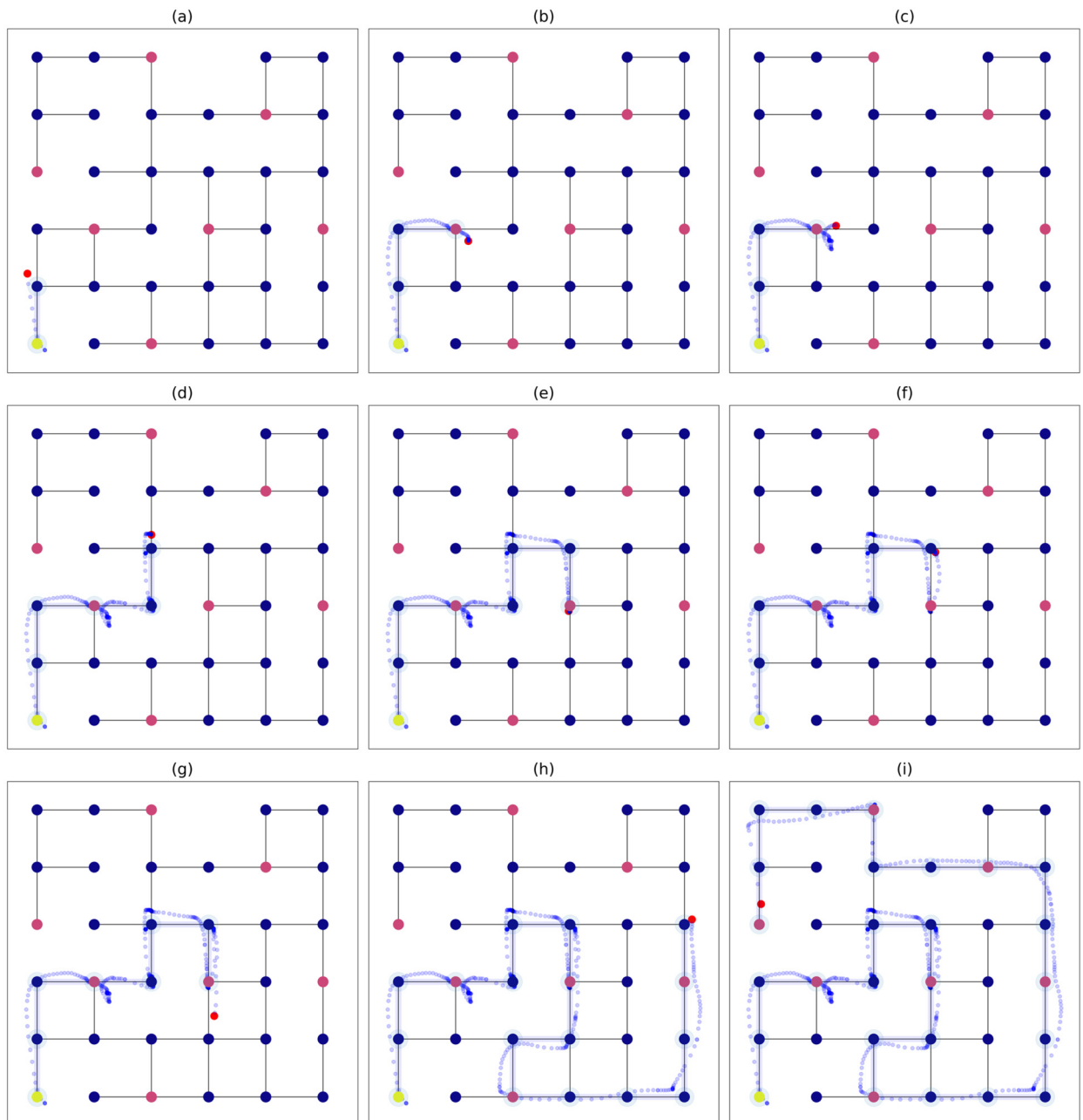


Fig. 1. The richness of movement kinematics data during the solution of a problem-solving task, which requires participants to find a path that starts from the yellow node and passes through all the red nodes, without crossing any node twice [33]. The nine panels show the time course of the movements, from the beginning (a) to the end (i) of the task. The finger trajectory is shown with small blue circles (whose density indexes movement velocity) and the currently selected path is highlighted in gray. See the main text for explanation.

[48–50]; as such, understanding this sort of behavior is central to the study of what the brain does and why [51]. Studying neuronal dynamics in very restricted or artificial settings is instructive but cannot tell the whole story: in the long run, it could hide important aspects of brain processing that depend on the particular conditions (or “natural statistics”) in which it evolved and now operates. In other words, a deep understanding of the brain cannot disregard the conditions that promoted its evolution, as it is in these conditions that brain dynamics acquired their meaning.

Fourth, the structure of experimental studies in the laboratory is often rigid and risks oversight of some fundamental aspects of behavior and cognition. The usual strategy followed in laboratory experiments is to present stimuli in trials and blocks and then measure simple behavioral responses to the stimuli, such as choices and reaction times. However, many of the “natural” circumstances that elicit behavior are inherently different than those experimental circumstances. For example, driving and navigation are continuous tasks and hence defining the beginning and the end of a trial, or of activities like “entering a new lane” for a driver or “encountering a fork in the road” for a navigator is largely arbitrary. Relatedly, the construct of a “stimulus onset” that is so methodologically convenient to calculate reaction times breaks down when it comes to naturalistic behavior. Except in limited conditions, considering the decisions of drivers and navigators as “responses” to external stimuli that have some clear onset ignores the realities of temporal sensory dynamics. Prior work has proposed the use of models that keep track of the continuous estimation of affordances and how they change over time to address such limitations [6,20].

Fifth, and perhaps most importantly, behavior is not just a way of expressing the output of cognitive processing, but part and parcel of it. A methodological (and sometimes conceptual) cornerstone of many studies in the laboratory is that stimuli are the “inputs” of cognition and behavior is its “output”, which – along with neuronal activations – can be measured. A reason why this input-output distinction works is because laboratory studies artificially break the link between action and subsequent perception that is instead mandatory during ecologically valid behavior [45]. However, a fundamental lesson of ecological, situated and embodied studies of cognition is that this distinction is severely limiting when considering naturalistic animal-environment exchanges dominated by feedback interactions [52–59]. During situated studies that involve living organisms or robots, and in which action-perception contingencies are preserved, it is common to observe that motor actions also influence decision-making processes rather than only the other way around [60–62]. For example, when participants performed a random dot motion decision task that required them to reach a left or a right target with an arm, and the motor costs to reach the two targets differed, they showed a bias towards the less costly action [63].

Other studies in naturalistic settings revealed that the interaction between perceptual, motor and cognitive processes could be much richer than traditionally considered. For example, they revealed that sensing is active and determined by internal predictions and goals [64–68], that some cognitive processes are offloaded to the external world [69–72] and that perception, decision-making, memory and other cognitive processes benefit from sensorimotor strategies that are hard to identify (or even to hypothesize about) using standard settings [73–75]. Furthermore, theoretical and formal studies in psychology and motor control reveal that the action system is cognitively sophisticated [76,77] and better described as a flexible decision-making system than as a passive executor of motor commands generated by a putative “central executive” [78–82]. Taken together, these lines of research (and others) suggest that behavior is a rich topic in itself, and is widely interconnected with the study of cognitive processing in humans and other animals.

3. The importance of using sophisticated models to study rich behavior: some examples

So far, we discussed the benefits of studying rich and ecologically valid forms of behavior to advance psychology and neuroscience research. Clearly, leaving the comfort zone of simple laboratory experiments requires a careful consideration of the challenges that arise to study, analyze, model and ultimately understand behavior “in the wild”. These challenges include design issues, such as the realization of setups that permit studying naturalistic behaviors of individuals and groups in ways that are tailored to the research questions; technical issues, such as setting up recording systems that afford a robust monitoring of the variables of interest; methodological issues, such as ensuring that the experiment collects enough data points to test hypotheses robustly, and selecting the best formal and computational approaches to analyze rich datasets.

We are witnessing significant progress in each of these challenges. Technical advances, reduced costs, and widening availability have all contributed to an array of opportunities to use immersive virtual reality (VR) as well as mobile games, to study rich behavioral patterns, such as body, hand, head, and eye movements during naturalistic conditions. Some devices that we use every day, such as smartphones, include tools like accelerometers, gyroscopes and GPS that permit recording rich forms of behavior for prolonged periods of time. Many technology companies are already using everyday devices, such as smartphones, wearable electronics, and vehicles to collect “big data” on human behavior - in the widest possible sense, from spatial navigation data to discussions in social networks. Partnerships between academics and tech companies can in some cases [83] result in publicly sharing behavioral (and other) data and insights that might otherwise be kept private. The richness of these data offers countless opportunities to address important

cognitive questions (e.g., about spatial navigation, planning, decision-making, opinion dynamics) in ecological, and large-scale, conditions. Similarly, advances in virtual reality have made available easy-to-use, low-cost and highly precise tracking devices, like built-in immersive VR headsets, trackers and controllers, which enable researchers to collect large biometric datasets for the study of human motor behavior in increasingly convincing simulated environments [226]. Finally, portable neural recording techniques are increasingly available that can capture brain signals during naturalistic behavior of humans (e.g., portable EEG, fNIRS and MEG, [84,85]) and other animals (e.g., multi-unit recordings), sometimes for prolonged periods of time. Some advanced methodologies are now available to follow freely moving animals [86] including humans [87] in naturalistic settings and virtual reality environments [88,89] that can be exploited to design innovative experiments and potentially to collect large, diverse datasets [90].

While all these advances are important and exciting, we argue that developing sophisticated models of behavior plays a particularly important enabling role in the study of ecologically valid behaviors outside the rigid constraints of laboratory experiments. This is because ecological behavior and rigorous experimental analyses can sometimes reveal opposing requirements. The former is largely unconstrained and highly variable and requires dealing with multiple interacting variables whose (causal) relations are difficult to assess. Rather, the latter typically requires the identification of a few quantitative variables that can be measured precisely, manipulated and compared with statistical tools. Bridging this gap is notoriously challenging and this fundamental problem has discouraged the study of rich forms of behavior to date. The importance of sophisticated computational models lies in the possibility to bridge this gap, by capturing the richness and variability of naturalistic behavior and distilling it in a formally sound way. In turn, this might render naturalistic behavior amenable to sound quantitative research.

To illustrate the ways “sophisticated behavioral models” could help align ecological validity and methodological rigor in the study of rich behavior, Fig. 2 shows three examples from psychology, neuroscience and sports analytics, respectively. The model shown in Fig. 2a (left panel) is a simple state-transition diagram (or finite-state machine), akin to an ethogram, that describes the sequences of the discrete motor states characterizing the observed behavior of *C. elegans* (forward and backward locomotion, ventral and dorsal turns, reversals). In their study, Kato et al. [91] showed how state-transitions in the animal motor behavior are well aligned with the global neural dynamics of the animal. The testing of this hypothesis required a low dimensional representation of the neural activity that was recorded from the entire neural population of the animal. Standard principal component analysis (PCA) was used to obtain low-dimensional descriptions of the global neural activity. The brain-wide activity of *C. elegans* was shown to consist in cyclic trajectories occupying a sub-space of the PCA state-space (a manifold), with specific tracts corresponding to specific motor states and the transitions/bifurcations between them reflecting the state-transitions observed in the behavior. Crucially, this was shown to be true both when the animal is active and when it is immobilized. Applied to the same data, a different model based on a coupling between dimensionality reduction and stochastic system dynamics was able to predict switches between behavioral states based on the measured neural activity, both within and across individual worms [92]. Coupled with sophisticated motion capture and kinematic reconstruction techniques, a similar type of analysis has also been used to describe the behavior of freely moving monkeys [93]. This type of models, based on a combination of dimensionality reduction techniques and state-transition diagrams, exemplifies our view that a sophisticated model is not necessarily one with complex methods or multiple variables, but rather one that helps characterize rich behavior.

The model in Fig. 2b is a Bayesian nonparametric method (called a Gaussian Process - GP) used to formally characterize and predict the movement trajectories of humans playing a simple pong-like game on a computer screen: one player controls (vertically) the trajectory of the “ball” (moving horizontally at constant speed) with the aim of scoring a goal against another human player, or a computer, who controls a bar acting as a goalie [94]. While players control the continuous trajectory of the ball, their input to the game simply consists of a sequence of discrete choices (i.e., changes in vertical direction). This enables the modeling and prediction of continuous trajectories as a sequence of discrete decisions generating a rich dynamic. Data from real plays were used to train a model of the “ball player” able to predict the probability of switching directions at any given time of the game as a function of the game’s state and of the goalie’s identity. Another similar GP model was trained to quantify the expected value of switching directions at any time throughout the trial. Being able to simulate artificial trajectories as the results of discrete decisions, informed by dynamic interactions with the environment and by online estimates of choice value, made it possible to identify individual strategies and to quantify the coupling between agents. This could be achieved by performing side-by-side comparisons of data simulated in different configurations with data from real participants. It was demonstrated that higher-scoring participants changed their movement direction when it was most effective to defy the other player’s

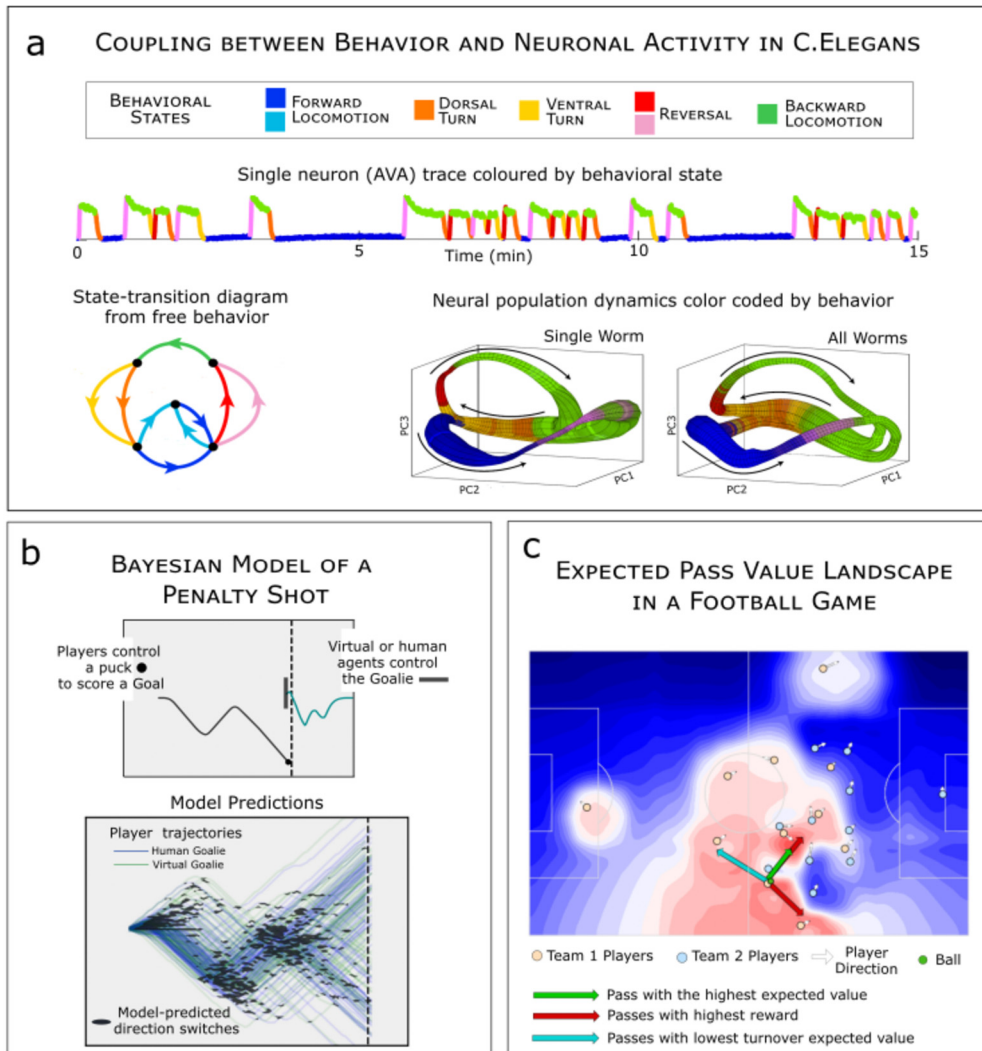


Fig. 2. Three examples of “sophisticated models” to study rich forms of behavior and their neuro-computational mechanisms (a) A schematic view – adapted from [91] and [92] – of the methodology associating motor behavior to neural activity in *C. Elegans*. The free motor behavior of the animal is described by a state-transition diagram (lower left panel) between the observed discrete behavioral states (upper panel). The global neural activity, characterized by a low-dimensional dynamics in the PCA space (lower right panels), is associated to behavioral states based on the segmentation of the neural trace of the AVA neuron (middle panel) most representative of the first PC vector. A model based on Diffusion Mapping [92] showed the global dynamics to be invariant across animals. (b) Schematic view of a “pong” game – modified from [94] – in which players have to score a goal against an artificial or human controlled opponent (upper panel). Real player’s trajectories (blue and green lines in the lower panel) are used to train a non-parametric Bayesian predictive model that generates trajectories by computing the most probable points of switch in puck direction (black patches in the lower panel). (c) Schematic illustration – adapted from [38] – of the decision surface of a soccer player (green circle) who has to decide to whom to pass the ball during a game. This “embodied decision-making” model predicts which are the passes with the highest values (i.e., probability to score a goal), the highest rewards and the lower turnover. These illustrations exemplify the advantages of modeling rich behavior to advance our knowledge of brain processing (Fig. 2a) and of human strategies (Figs. 1b and 1c) during real-world tasks.

defensive strategy, whereas lower-scoring participants were less precise in selecting the most opportune moment to change direction. In short, a model able to link the decision-making process to the dynamics of the environment and the value of instantaneous decisions made it possible to gain insights into a complex interacting task that would have otherwise been inaccessible.

Another representative example of a sophisticated model that supports the study of rich behavior is depicted in Fig. 2c, which shows a schematic illustration of the “utility surface” of a soccer player (green circle from which the arrows start) who has to decide to which teammate it is most useful to pass the ball during a soccer game [38].

The utility surface shown in the figure is calculated by a computational model that jointly considers several factors, such as the probability that the pass to different teammates will be successful as a function of distance and number of opponents in the surroundings, as well as the value of passing the ball to each location (which is positive if the pass increases the probability that the team will score a goal, and negative if the pass increases the probability of a “turnover” and that the opposing team will score a goal). Some factors of this utility surface are learned with machine learning techniques using large datasets of actual games (e.g., the probability that a player will score a goal from any position in the game field), whereas other factors are described analytically (e.g., the fact that the value of locations is higher in the opponents’ side of the game field).

The “sophisticated model” used in this latter example (and similar models of other sports like basketball [37,38]) permits mapping a continuous “embodied choice” problem (deciding to whom to pass the ball) into the usual dimensions considered in economic choices (utilities and probabilities), hence aligning the two domains. What makes embodied choices different from standard economic choices is that calculating choice dimensions like utilities and probabilities requires consideration of geometric and situated variables, such as distances from teammates and opponents (which in turn requires a sophisticated statistical model). However, once the choice dimensions have been calculated, it is possible to treat an embodied choice like a risk-based economic choice: as a competition between choice alternatives, such as the “safer” choice with the highest utility, the “riskier” choice with lower probability of a turnover, and so on (see the arrows in Fig. 2c). It is also interesting to note that while the utility surface of Fig. 2c is continuous, it has few maxima (the points in dark red) – hence it is possible to assume that while the soccer player has (in principle) nearly countless options, he or she should optimally deliberate between just a few of them. The methods illustrated in this example are therefore potentially useful for the analysis of other embodied decision tasks, such as deciding which stones to use to cross a river or which holds to use to climb a wall [20].

The three examples shown in Fig. 2 help illustrate at least four ways in which sophisticated behavioral models can help study rich behavior outside the laboratory. First, models provide a succinct (often, low dimensional) formal characterization of behavior. For example, in Fig. 2a, sequences of rich behaviors, such as turns and forward movements, are represented as finite states that abstract away from many details and only encode what is most critical for the analysis, e.g., the probability of making transitions from one behavior to the next. Of note, in the study illustrated in Fig. 2a, not just behavior but also neuronal activity is analyzed with the aid of a model – in this case, characterizing cycling neural dynamics by applying principal component analysis to the time derivatives of neural traces. This makes it possible to test hypotheses on how the activity of specific neurons or circuits may govern the transitions between behaviors versus controlling the details of each. In Fig. 2b, behavioral trajectories – which are originally vectors of X and Y values that change over time – are summarized by a compact (Gaussian) representation of switches in Y direction that greatly simplifies the analysis (possible also thanks to an intrinsic regularity of the task, which is a constant speed in the X direction). This was used to reveal how performance was related to specific strategies used by participants.

A second related point is that computational models can help decompose and formalize rich forms of behavior that arise in embodied settings into the very same factors that are usually considered in laboratory studies, hence aligning the two settings. One example is the model shown in Fig. 2c, which addresses an embodied choice situation (i.e., passing the ball) but decomposes it into the utilities and probabilities often considered in economic decisions [20].

Third, computational models help identify *latent variables* that extend the scope of the quantitative analysis beyond standard measures such as reaction times or movement kinematics. For example, the computational model of Fig. 2b is used to identify the change points that are the dependent variables for the subsequent comparison between higher-scoring and lower-scoring participants. A wide literature in computational modeling shows that once identified, such latent variables can be used for multiple purposes. For example, latent variables identified with a model that only has access to behavioral data can be used as predictors of neuronal activity, on a trial-by-trial basis [95–97]. Furthermore, latent variables can be used for “computational phenotyping” and the identification of individual factors or group differences, as in the case of the comparison between higher-scoring and lower-scoring participants in [94] or the classification of participants as belonging to “normal” or “patient” groups in computational psychiatry [68,98,99].

Fourth, some computational models are *generative* and permit not only an analysis of existing data but also synthesis of new data that are statistically similar to (or predict) missing data, such as for example the behavior of non-observed players in the football behavior prediction model of [100]. The possibility to simulate and synthesize the behavior of interest paves the way for a variety of model uses beyond data analysis. These include testing to what extent the model generalizes to novel situations, which in turn can inspire novel hypothesis-driven experiments, or

implementing artificial systems that closely mimic human or animal behavior (e.g. to score participants' abilities, or support AI-based "synthetic opponents" in multiplayer experiments).

The above selected examples help appreciate some of the ways sophisticated behavioral models can help us study rich behavior outside restricted laboratory settings and demonstrate a range of possible methodologies to develop them. However, the list of benefits and methodologies is by no means exhaustive. In the next section, we provide a more systematic overview of sophisticated models of behavior that have been developed within – or that could be adapted from – many fields, such as statistics, control theory, reinforcement learning, artificial intelligence, and others.

4. Successful applications of sophisticated methods and models to study rich behavior

The three studies that we highlighted in Fig. 2 illustrate a growing interest around the study and modeling of rich behavior in psychology, neuroscience and other fields, such as sports analytics, ethology and robotics. In this section, we more systematically review some studies in these domains that have developed useful methods (designs, recording and analysis techniques, computational models, etc.) for the study of rich behavior. We focus in particular on studies that included sophisticated behavioral models, which we consider key to advance the field.

4.1. The study of rich behavior in motor control and skill acquisitions

The field of motor control has traditionally focused on the study of short movement sequences – like reaching and pointing – or of rhythmic whole-body motor behavior – like gait – that can be described with a small number of parameters. In recent years, however, research in motor control has approached more complex forms of motor behavior, skill acquisition and motor development, with the aid of new methods of analysis and new models, borrowed in some cases from fields like sports science and machine learning.

An important advance has come from the adoption and development of dimensionality reduction techniques that allow the unbiased characterization of whole-body kinematics of complex asymmetric and non-cyclic actions like tennis serves [101] or overarm throws [102,103]. Importantly, these low-dimensional descriptions of complex motor actions support the exploration of complementary aspects, like the characterization of the action's outcome (e.g., the direction of the propelled ball) and its predictability. In the work of [103] a spatiotemporal principal components decomposition of whole-body throwing kinematics allowed the unbiased characterization of individual strategies in a population of non-trained adults, and the identification of four main strategies, reoccurring across individuals, that resemble the different phases of throwing skill acquisition during development. The adoption of similar approaches has seen a surge in motor control studies and is expected to gain further importance in synergy with the increasing interest in the search of regularities and patterns in complex systems across several research fields [104]. A complementary approach to achieve compact representations of complex motor actions is the "kinectome", defined as the network with nodes representing body points and edges the correlations of the accelerations between each pair of body points [105]. This approach opens the possibility to use graph theory methods for an unbiased analysis of whole-body kinematics: e.g., it allowed detecting early onsets of motor impairments from gait recordings.

From a broader perspective, dimensionality reduction techniques have been shown to be highly valuable for the study of complex whole-body motor behavior. This is because of their ability to extract compact descriptions of high-dimensional kinematics data, which can bypass the need to pre-select variables of interest a priori. This in turn paves the way for the study of naturalistic motor behavior and its connection to cognition in a quantitative manner. A clear example of this is the application of dimensionality reduction techniques to characterize the amount of information about an agent's intention that is embedded in the kinematics of observed actions - e.g., for reaching [106] or full-body throwing [102]. This characterization supported the principled design of experiments for the study of interpersonal sensorimotor interactions in naturalistic settings [34,107]. In one study, knowledge about the spatiotemporal encoding of intention in reaching actions (reaching for a bottle to pour or to drink) was used to compute the amount of information that could be actually extracted by an ideal observer (a trained decoder) and to compare it with human performance [108]. This study concluded that humans could infer intentions based on the reading out of information encoded in the observed kinematics, with a confidence that reflects the amount of information available. In [107], the low-dimensional characterization of predictability profiles and individual motor strategies [102,103] enabled a behavioral assessment of human predictions based on the observation of biological motion for the case of unconstrained overarm throwing, and show that humans not only are able to extract information from observed actions in the case

of complex behaviors (like throwing) but they are also able to use this information online to optimize their interaction with the dynamic environment in which they act.

With the advent of new technologies, laboratory setups can now integrate a range of devices including full-body kinematics, force sensors and platforms, haptic devices and immersive virtual screens, thus enabling the exploration of novel research questions. Investigating the manipulation of objects with complex non-linear dynamics provides an ideal example. One study investigated the mechanisms that allow humans to seamlessly transport a cup full of fluid without spilling its contents – a task in which reciprocal interaction forces between the actor and the object can easily generate chaotic (and hence unpredictable) behavior [109]. This study showed that actors prepare the transportation task by creating initial conditions that stabilize the internal dynamic of the fluid to a predictable steady state, thus allowing for an efficient feedforward control. A similar conclusion was obtained in a study investigating the precise control of a whip, a dynamical system with virtually infinite degrees of freedom [110]. In this case too, results showed how, despite the large individual differences in the adopted motor strategies, an efficient control of the whip always relied on the control of a few key parameters of the whip's dynamics that can suppress chaotic behavior and make its trajectory predictable. These insights were achieved by taking a “task-dynamic” approach in which an object dynamic is modeled (e.g., with physics simulators or contraction theory) to identify key parameters whose tuning can bring to stable and predictable dynamics. Comparing dynamic model predictions with human performance then allows one to characterize human strategies and interindividual differences that would otherwise go overlooked; see also [111–113].

Sophisticated analytical and computational models have also been crucial for gaining insights into how humans select optimal strategies when having to execute accurate movements despite the intrinsic sensorimotor variability that characterizes the central nervous system. Of particular interest is the case of redundant motor tasks. As for most daily actions, in a task with redundant degrees of freedom, the same outcome can be achieved with different actions – which poses the question of how to choose the optimal motor strategy. To approach this problem, different methods have been proposed that characterize the geometry of the redundant mapping between action variables (e.g., the ball release position and speed in a throwing task) and the action outcome (e.g., the score or distance from the target) [114–117]. These geometric mappings can be seen as landscapes where optimal solutions are represented by low dimensional manifolds (i.e., sub-spaces), in which gradients along different directions (e.g., how fast the score changes when varying a given action's parameter) quantify the tolerance of the task to the corresponding motor noise. These methods have shown that skilled motor performance relies on the “shaping” of intrinsic motor variability so that the latter falls mostly into directions that do not affect the desired outcome, thus reducing variability along the directions that matter most [118,119]. This work supported the exploration of the individual strategies that emerge during the learning of new motor skills. In particular, a computational approach known as Tolerance-Noise-Covariance (TNC) was used to show that when learning a throwing task subject to non-standard dynamics (the skittle – a ball attached to a fixed pole with a wire that has to be thrown to hit a target), participants typically shifted their average action towards high tolerance regions of the action-to-outcome mapping, and concurrently oriented the covariance of the motor noise in the direction of the solution manifold [115]. The geometry of the action-to-outcome mapping in a similar motor task has been further exploited by introducing model-based performance variables quantifying errors and tolerance in the timing of ball release, based on the geometrical relation between the action trajectories (i.e., its temporal unfolding) and the underlying task's landscape (i.e., the action-to-outcome mapping). This revealed timing strategies adopted at a single-trial basis, complementary to those emerging from the TNC analysis. An analytic alternative to TNC based on a Hessian decomposition of throwing performance was also proposed [117], which applied similar analyses to higher dimensional tasks. These studies highlight the importance of mathematical and computational models for the study of individual strategies and learning of motor tasks which require the control of multiple variables. Another interesting research line proposes complementary approaches for the study of motor learning and motor augmentation, exploring the possibility to exploit the muscle-to-force null space for learning the control of extra-degrees of freedom. Seminal studies, integrating machine learning and information-theoretic methods, have shown that null space control is feasible [120] and that it can support the control of virtual and/or robotic end-effectors [121].

4.2. *The study of rich behavior in psychology*

While motor behavior has long been neglected in psychology [9], there is a recent trend towards increasing the complexity, variability and ecological validity of both stimuli and participants' responses in psychological studies [2,20,122,123].

A promising way forward in this direction consists in designing “classical” tasks, such as two-alternative forced choices (2AFC), but collecting richer behavioral data, such as kinematic or eye tracking data, which reveal underlying choice dynamics and the temporal evolution of cognitive variables, such as choice uncertainty [21,22] and confidence [28]. These rich data collected across perceptual [25] and economic decisions [124] can subsequently be analyzed using “embodied choice” models [60,82] that extend classical models of decision-making, such as drift-diffusion [125], to also include movement dynamics.

Interestingly, unlike traditional models that describe decisions as serial (perception-decision-action) processes, embodied choice models inherently include feedback from action dynamics to perceptual and decision processes. Therefore, using these models for data analysis automatically entails a conceptual departure from serial models and some commitment to the idea that action is part and parcel of cognition (a recurring theme in this review). A recent study illustrates this point by augmenting the drift-diffusion model in a 2AFC task, integrating information by visual fixation and adjusting the Gaussian Process dynamics accordingly [126]. By doing so, the model can make predictions about the relationship between (temporal) visual attention patterns and choice results: e.g., it is shown that the last fixation is predictive of choice, and that exogenous manipulation of the relative fixations on two options can bias the final choice.

Notably, the approach described here is not limited to simple 2AFC paradigms but can address more complex ones, such as sequential choices, which are also ubiquitous in real-world settings, and therefore critical to an improved understanding of rich naturalistic behavior. For example, a study performed by [127] tracked movement kinematics during a reaching task in which human participants had to perform sequential choices, and used multiple computational models of multistep choices to infer their strategies. This study revealed that people tend to pass from a first phase in which they choose based on the average reward across future options becoming available, to a second phase in which they choose based on maximizing reward. Another study that used a similar approach revealed that people prefer options that make more future options available, above and beyond utility concerns; and that the availability of options positively influenced participants’ perceived freedom of choice [128]. This resonates with findings from a recent model based on an information theoretic approach [129], which shows that endowing agents with the tendency to maximize the foreseen occupancy of their future actions and states can account for a range of complex behaviors with no need to invoke reward seeking.

The studies reviewed above still exemplify relatively simple choice situations, with only a few predefined options. Other studies have tried to progressively relax the constraints of laboratory experiments and to address tasks that include increasingly naturalistic features. One study used the analysis of tracked kinematics to ask how people make reaching decisions when they are already tracking a potential “prey” and a novel opportunity arises, i.e., another “prey” appears [130]. Another showed that decisions made while walking depend strongly on the phase of stepping [131]. Such decide-while-acting paradigms are significantly different from standard experimental paradigms in which choices are static and the set of choice options is predetermined and fixed; they are more representative of naturalistic situations in which opportunities appear or disappear, both as a function of the animal’s actions and spontaneously [132]. Importantly, these kinds of scenarios are incompatible with the classical notion that deliberation ends and action begins when neural activity reaches some kind of “decision threshold,” because if actions are being performed then some threshold must already have been reached while deliberation about a new opportunity takes place. This forces us to generalize the concepts of deliberation and action into a framework in which deliberation about options, commitment to an action choice, and decisions to switch from one action to another can all be described as state transitions within an integrated dynamical system. We will discuss some neural studies supporting such frameworks below, in section 4.3.

Another experimental direction has aimed at capturing the nuances of delayed feedback in modern naturalistic tasks such as many-alternative choices, in which fixed available resources (finite-capacity) can be spread across multiple options (breadth) or focused more attentively on a subset of those (depth). A finite-sample capacity model formalized to inspect this breadth-depth dilemma [133] found that for small capacity the optimal strategy favors broad search (drawing one sample per alternative), while when the capacity increases the best options turn in favor of a depth search of few alternatives. Interestingly, these model predictions inspired an experimental study that tested and confirmed the predictions validating the model [134], thus providing new insights into the cognitive processes involved in daily-life decision-making tasks.

Another important, yet historically underexplored dimension, are reward-driven decisions which involve the interplay of reward values, learned expectations (and therefore prediction errors) and individuals’ receptivity to reward,

which varies throughout the day. A recent model proposed two parallel learning processes—one fast and relatively quickly forgotten, and the other slower and longer-lasting—which best explain variance in physiological reward prediction errors (as decoded from heart rate and EEG signals) across a multi-day remote study [135].

Gross, complex embodied dynamics are particularly visible as people move around the world. Several virtual navigation studies in 3D “mazes” have asked how people make the continuous navigational decisions required for such daily activities. One such study reported that a specific left-right head-scanning movement (“vicarious trial and error”) that indexes “mental exploration” at choice points is predictive of navigation performance [136]. Another study used a computational approach to study how participants combine landmark information and path integration mechanisms during a homing task that required navigating into an environment and then returning to a home location [137]. The experimenters designed a Bayesian model of optimal control under various sources of uncertainty, related to variability in perception, action and internal representations – and found that all these sources of uncertainty are necessary to appropriately explain endpoint variability and common navigational errors. Another study showed that people are able to flexibly decide between habitual routes and shortcuts when provided with different instructions [138]. The same data were re-analyzed using an information-theoretic computational model (Information reinforcement learning, InfoRL) to quantify the amount of cognitive resources required to form each plan and how optimally these resources were invested [139]. This re-analysis indicates that not only do people selecting shortcuts invest greater cognitive effort, but they also make less efficient use of cognitive resources, despite following routes that may seem advantageous. A large scale study of spatial navigation in a videogame demonstrated how navigation skills are modulated by the interplay of cultural factors and individual factors (like gender and age), with patterns of navigation abilities across the globe which have been shaped by economic wealth and gender inequalities [140]. Other on-going work is attempting to gather more insights from these datasets using sophisticated models such as the InfoRL adopted in [139].

Complementary to studies exploring navigation in virtual environments, another set of studies addresses cognitive questions using large scale, real-world data that were not originally collected for research purposes. A large scale study of navigation with real-world GPS data collected through an app, used a vector-based model reproducing human navigation strategies better than previous work employing path-length minimization, or on the maximization of the first straight segment path [83].

A general approach to the study of rich behavioral patterns in game-like settings consists of designing *generative models* of the same behavior, using methods from artificial intelligence, machine learning and related fields (see below for a discussion of robotics models). This approach permits a side-by-side comparison of behavior between computational models and participants dealing with the same sequences of observations and actions in the experiment. This technique enables inferences about which type of model and which parameters best account for individual behavior, i.e., “computational phenotyping” [98,141]. One example of this approach, and the use of AI systems to emulate cognitive and neural processes in ecologically valid tasks, is the study of [142]. The authors considered to what extent the behavior of humans (and monkeys) during ball tracking could be modeled by various recurrent neural networks (RNNs), with and without the ability to simulate the future position of the ball. The RNNs endowed with simulation mechanisms provided a better account of the behavior and of some of the systematic biases seen in humans (and monkeys), supporting the idea that primates can use mental simulation to better track and intercept balls.

Various studies have used probabilistic (generative) models of body kinematics to infer movement intentions during reaching actions in 2D [143] and 3D paradigms [144]. Others have used sophisticated generative models of game dynamics (game physics engines, which model the rich dynamical properties and relations between everyday objects) to explain intuitive physical judgments in infants and adults, such as whether a stack of dishes is stable or will topple [145,146]. In some cases, generative cognitive models enable simulations of complex behavior measures, such as eye movements. As one example, a Dynamic Bayesian Network (DBN) was used as a task-independent representation of cognitive state, and played the role of a bias for the production of saccades in a human visual search study [147]. The DBN learned conditional probabilities governing saccade attributes like velocity and duration, as well as transitions between cognitive states. This model was then leveraged to generate synthetic saccades across multiple task types, to be compared with statistics from human participants. Notably, this model affords additional validation by analysis of temporal dynamics such as return angle, which reflected patterns in the human data despite not being directly modeled. Other generative models have been designed to study the rich behavioral patterns that emerge during cooperative joint actions and to identify their associated cognitive mechanisms, such as predictive representations of others’ actions and intentions, shared task representations and roles that might emerge during the interaction (e.g., leader-follower relationships) [148–150]. For example, a model of Bayesian Delegation was able to make inferences similar to human

observers about the intentions of others, in a task in which multiple agents were required to cook a meal together [150].

As particularly visual creatures, most humans explore their world primarily through the control of visual attention, a fact that, when combined with an increasing variety and flexibility of eye tracking equipment, enables a diverse range of research inquiries relating to information sampling, planning, and attention. Studies have recently addressed the rich patterns of eye movements observed during everyday tasks, such as when making a cup of coffee, watching others' actions, or viewing paintings [64–68]. For example, one study recorded body and eye movements of participants that navigated in a virtual environment and were asked to approach or avoid objects along the way [151]. This study revealed that the fixation locations on objects were task-dependent rather than depending on the (fixed) bottom-up saliency of visual inputs. Another study asked how eye movements are planned in tasks that require making multiple actions – and used a series of computational models to ask whether participants can optimally plan sequences of eye fixations in advance, as opposed to just the next fixation [152]. This study found that a probabilistic planning model best predicted the location of the first fixations, suggesting that participants might plan multiple eye movements in advance in statistically optimal ways.

Another study asked a question often addressed in decision-making – namely, how participants balance the costs and benefits of their decisions – but in the context of a sensorimotor task resembling dart throwing [153]. Participants had to hit a circular green target with their finger, in order to earn points; but simultaneously they had to avoid touching a red target, partially overlapping with the green circle, which was associated with a penalty. In different trials, the distance between the two targets and the penalty from the red target were varied, therefore creating different cost-benefit configurations. Furthermore, movement variability was manipulated by displacing the visual feedback of the participants' hand (which was shown in a mirror) with respect to the actual movement arm (which participants could not see). The optimal strategy in each trial (estimated through a statistical model) therefore depended on the cost-benefit configuration and on the variability of the movement of each specific participant. The higher the penalty and/or the participants' movement variability, the more he or she needed to move away from the red target. The results of the study show that when deciding where to aim, participants took into account – in a statistically sound way – both the magnitude of the penalty and the uncertainty associated with their movement variability.

4.3. *The study of rich behavior in neuroscience*

It is becoming increasingly clear that advancing neuroscience requires incorporating behavior more seriously [39]. This “neuroethological turn” promotes the study of the neuronal foundations of natural behaviors, such as foraging and social interactions [19,154].

Considerations of natural behavior in neuroscience force one to blur the conceptual borders between putatively distinct psychological processes such as perception, cognition, and action. In particular, many neurophysiological studies of decision-making have shown that the neural correlates of “decision variables” are found in regions of the brain that are also clearly implicated in sensorimotor control, including the parietal cortex [155,156], frontal eye fields [157], premotor cortex [158], basal ganglia [159,160], and even the primary motor cortex [161] and superior colliculus [162], two structures just a few synapses away from muscles. These findings have led to proposals that decisions, at least those that involve a choice between actions, emerge not through abstract cognitive processes, but through a competition between candidate actions [163–166]. For example, the “affordance competition hypothesis” [163,167] proposes that neural activity in the “dorsal visual stream” of the cerebral cortex [168] uses spatial visual information to specify multiple potential actions (“affordances”) whose neural representations compete against each other through mutual inhibition. That competition is biased by all the various factors relevant to the choice, and continues until one of the action representations suppresses the others and is thus selected for execution. This explains the prevalence of decision variables throughout the sensorimotor system and suggests how deciding and acting could unfold in parallel. In particular, neurophysiological recording studies suggest that the dorsal premotor cortex may be a key node in that competition, effectively implementing the type of “utility surface” described above in Figure 2c [158,169]. Subsequent studies suggest that this surface is continuously updated as sensory information changes [161], reflecting the process of deliberation. Further, a variety of evidence accumulation models have been used to illustrate the role of representations of confidence during deliberation [170], such as neurons in the lateral intraparietal cortex that predict avoidance of a challenging binary choice [171]. This class of models has also been used to hone in on trial-level learning dynamics [172], showing how learning happens earlier than estimated by classical approaches, and that strategies

such as “lose-shift” and “win-stay” are sometimes deployed independently rather than complementarily. Importantly, this process can continue even while the sensorimotor system is engaged in controlling a given action, because other possible actions can still be specified and the system can switch to them if circumstances suddenly change. A recent analysis using dimensionality reduction of neural activity recorded in motor, premotor, and prefrontal cortex, as well as the basal ganglia, suggests that all of these regions form an integrated dynamical system that implements deliberation, commitment, and movement control in a unified fashion [173]. Within that system, deliberation can be described as shifting the neural state within a particular subspace (a “decision manifold”) and commitment to action as falling off that manifold into a choice-dependent subspace. Importantly, while different brain regions emphasize different aspects of the deliberation process (evidence in prefrontal cortex, speed-accuracy control in basal ganglia) the system unfolds in a unified fashion without specific “clusters” of neurons responsible for deciding versus acting. This dynamical description thus addresses the challenge, posed above in section 4.2, on how decisions and actions can be seen as state transitions within a single, integrated dynamical system that can perform all of these functions in parallel and in a constantly changing environment. More broadly, the recent trend to characterize mathematically the neural manifolds and the geometric structure of neural population activity holds the promise to shed new light on the function of brain networks, such as how they form topological representations underlying cognitive maps or abstract task representations underlying higher-order cognitive tasks [174].

A valuable additional perspective on rich behavior [2] comes from studies of neural and physiological responses while perceiving naturalistic scenes, e.g., while listening to a story or watching movies [2,175,176]. In one of these studies, eye-tracking and fMRI scans were collected from fans who watched basketball matches with the aim of inspecting neural and pupillometric responses in relation to surprising in-game events [177]. Surprise was quantified as changes in win probability with sport analytics techniques by training a win probability model based on a large corpus of games. fMRI responses were segmented into discrete states and shifts between them were modeled with an Hidden Markov Model (HMM) specifically implemented to unravel event structure from neural responses during naturalistic perception [178]. By comparing the outcomes of the two models, the study found that surprising events produced more frequent shifts in neural representations, increased pupil dilations, and enhanced memories of these events. Interestingly, these surprise responses were modulated by subjectively biased beliefs about winning probabilities. The same HMM segmentation of fMRI response has been deployed during movie watching to identify a nested hierarchical structure of fast-changing events (in sensory regions), and slower-changing events in higher-order regions [178] providing new insights into the course of naturalistic perception. Another study reported shared principles (e.g., next-word prediction before word onset) between brains and autoregressive deep language models (DLMs) in processing natural language, supporting the idea that these sophisticated models might be particularly appropriate to address the neural basis of language [227].

Another area of neuroscience in which the study of naturalistic behavior has always been at the forefront is spatial navigation, especially in rodents. Studies of rodent navigation have long adopted recordings of freely moving animals [179]. However, there have been relatively few attempts in neuroscience to formalize the rich patterns of behavior that rodents exhibit during spatial navigation. One such attempt includes the monitoring of head movements at decision points, which could be indicative of so-called “vicarious trial and error” and deliberation [180]. Other attempts include the development of formal methods to infer behavioral patterns [181,182], motor primitives and the grammar of movements [183–187] as well as energy functions [188]. All these methods, and others, can be potentially useful to align the rich behavioral patterns that we exhibit during navigation and other naturalistic tasks to the neuronal dynamics that we are increasingly able to record with high fidelity and at scale, hence providing a broader ecological context to neuroscientific questions.

The study of brain dynamics of primates has rarely considered naturalistic settings, but there are some noteworthy exceptions, such as the study of foraging [189], object tracking [190] and pursuit behavior in monkeys [191]. The study of [191] is particularly appealing as it exemplifies the usefulness of using sophisticated models to understand rich and naturalistic behavior. Here, rhesus macaques were trained to use a joystick to pursue artificial prey in a 2D environment. To understand the extent to which subjects anticipate future trajectories of prey, the authors compared several generative models making predictions about the direction of motion based on various sets of plausible inputs (e.g., Newtonian variables like position and velocity). By generating instantaneous directions of pursuit, these models produce complete trajectories that can be fit to empirical data. This approach suggested that monkeys make use of Newtonian variables (which are shown to be encoded in the dorsal anterior cingulate cortex) to make predictions about future prey locations during pursuit. More broadly, this study and others that focus on naturalistic settings can

provide a fresh view on cognitive operations such as decision-making; for example, they suggest seeing decisions as *continuous* cognitive operations that require the selection between ever-changing options and in which decisions and actions are interleaved [173,192].

Another way to bridge the gap between ethology and neuroscience is to align sophisticated behavioral patterns (e.g., ethograms) and neuronal dynamics when one or both are treated with analytical techniques (e.g., principal component analysis) for dimensionality reduction. We have already discussed in Fig. 2b one study using this approach, which shows that much of the brain dynamics of the *C. elegans* encodes and predicts transitions between simple behaviors, which are encoded even when the animal is immobilized and hence does not (fully) depend on external feedback [91,92]. Two other studies found that behavioral dynamics dominate brain activity (including spontaneous activity) to an extent that was not predicted by standard theories, which relegate behavior to the output stage of cognition [193,194].

4.4. The study of rich behavior in sports analytics, ethology and robotics

So far, we have focused on the study of rich behavior to address psychological and neuroscientific questions. However, there are several fields, like sports analytics, ethology and robotics, which study behavior for different purposes, but which have developed valuable methods that can be reused in psychology and neuroscience. While reviewing all the relevant work in each of these fields is impossible given space limitations, below we provide at least some pointers to orient the reader.

The field of sports analytics is quintessentially interested in extracting indexes and predictors of performance from large-scale, usually unconstrained streams of data collected during matches in individual sports like running or tennis, as well as team sports such as soccer and basketball. This has led to the development of useful techniques to measure and study sophisticated behavior during sports, which goes beyond classical discrete performance indexes, like ball possession or number of passes. Of particular interest is the case of team sports in which information from continuous spatiotemporal input (e.g. position and velocity) from multiple players are integrated with a cohort of interdependent discrete events (e.g., ball passes, shots, and rebounds), to dynamically quantify subtle aspects of the game. In the case of basketball, for example, Cervone et al. [37] adopted a multiresolution stochastic process approach to compute the Expected Value of Possession (EVP), a dynamic scalar value that quantifies the expected number of points a team will score during the unfolding of a given possession. In an alternative EVP estimate based on a deep learning approach, the model avails accurate predictions of micro-actions – specific decisions that a given player would make based on the previous events of the game. Similar approaches have been developed to represent relevant strategies and decision-making processes in soccer. The study shown in Fig. 2c provides an alternative example of how to compute the expected value of a possession in the context of soccer. Another approach consists of using sequential generative models of multiagent game dynamics (e.g., basketball) that explicitly model - and therefore permit inferring from data - ‘cognitive’ constructs that have interpretable semantics, such as individual goals and group strategies [195]. It is interesting to stress that this, as with other similar approaches, has the potential to address novel questions and characterize subtle aspects of the game, including decision-making strategies at the individual level [38], off-ball positioning strategies at the team level [196,197], and defensive techniques and performance [198]. It then appears clear that recent advances in sport analytics can be reused to address general research questions about cognitive processing, particularly for characterizing performance and decision strategies (at both individual and collective levels) in rich environments involving the context-constrained interactions of multiple agents.

The field of ethology offers complementary inspirations. Recent decades have seen a surge in extensive biologging techniques that allow studying rich behaviors of animals in the wild. Biologging refers to the use of miniaturized animal-borne sensors, ranging from GPS to physiological sensors and video cameras [199,200]. Detailed tracking data that could cover the animal lifespan are often integrated with data from other on-animal (e.g. physiological) sensors and remote sensing of the explored environment [201]. Ethologists can then address new questions, for example how navigation, foraging and hunting strategies are influenced by collective behavior [202] and individual decision-making [203], in interactions with the animal’s physiological state (e.g. fatigue or stress) [204] and properties of the environment (e.g., weather conditions) [205]. The use of animal-borne miniaturized video cameras [206] further enables the study of functional aspects of naturalistic animal behavior, like the case of tool manufacturing (e.g. hooked sticks), storage and use observed in New Caledonian crows when nurtured and living in the wild [207–209]. Alongside new opportunities for research, the advent of biologging practices in ethology has come with new challenges related

to the treatment and analysis of the large datasets they generate. This is prompting the development of new analytical approaches (e.g. state-space models) that can be combined with model-based predictions of animal behavior and of environmental information [210,211]. These developments can inspire new methodological approaches for the study of rich behavior in humans.

The field of robotics faces the challenge of realizing rich behavioral patterns in artificial systems with several degrees of freedom and can therefore offer conceptual and formal tools to the study of behavior in cognitive science. Of particular relevance are those branches of robotics that take some inspiration from biological control systems. One example is the idea that in both biological organisms and robotics, complex behavior is composed of motor primitives that function as building blocks [212,213]. One popular implementation of this idea in robotics is Dynamic Movement Primitives (DMPs): a formalism that is widely employed to enable robots to solve advanced motor control tasks, such as playing table tennis [214,215]. Progress in these and other formal methods developed to synthesize robot behavior can be redeployed to model and understand human movements.

Another robotic approach based on the Generative Body Kinematics model uses inverse planning and inverse body kinematics to infer the intention of human actors, such as for example which object they intend to grasp in a 3D environment that includes several potential targets and distractors [144]. Potentially, this generative approach can be used both to understand observed behavior and to synthesize adequate (e.g., complementary) actions in human-robot interaction studies.

Some robotics studies have explored the usefulness of endowing robots with the notion of affordances to address spatial navigation [216,217], grasping [218,219], and pushing [220] problems. These (and similar) robotic models may be reused to formally study the ways humans pick up and select between available affordances, as an alternative or together with the formal methods developed in sports analytics reviewed above.

Another interesting recent foray into integrating ethology-inspired methods with (neuro)-robotics and artificial intelligence is a 2019 paper that used deep reinforcement learning to train a physics simulation of an anatomically robust rodent [100]. The agent “embodied nervous system” was trained on a volley of naturalistic tasks familiar to rodent ethologists and neuroscientists (gap jumping, foraging, button pressing, and escape from challenging terrain), and the ensuing dynamics in the neural network (an architecture built from stacked LSTMs) was analyzed using adaptations of neuroscientific techniques such as perturbation. This work found two main classes of neural representations decomposed into task-specific encodings, and task-invariant behavioral kinematics encodings.

Finally, it is worth considering that the fields of robotics, brain-computer interfaces, and rehabilitation have developed several other methods for the modeling and analysis of complex movements, such as gait [221] and upper limb motion [222], or for stabilizing clinical brain-computer interfaces [223]. These are too numerous to be reviewed here but can enrich the toolbox of psychologists and neuroscientists interested in modeling sophisticated behavioral patterns.

4.5. Limitations of current approaches

In this section, we review various successful applications of innovative methods and models for the study of rich behavior. Despite the appeal of these “success cases,” it is clear that the field is still in its infancy and there are several remaining challenges to be met. One notable challenge is the complex trade-off between the development of increasingly sophisticated models, the range of phenomena that they can address, their interpretability and ultimately the benefits that they bring to psychology and neuroscience. This concern is especially relevant in this age of big data and of large scale, black box models, which can be powerful, but sometimes at the cost of transparency and interpretability.

Furthermore, it is almost impossible to capture all the complexities of real-life behavior, even by using the most sophisticated models. For example, the decision of where to pass the ball during a soccer game (Fig. 2c) depends not just on the chances of being successful and the utility of different passes, but on many other interrelated parameters, such as whether a team is leading in the scores or behind at the time of the pass, the time left in the match, the importance of the game (e.g. a cup final), as well as individual and social factors, not just in terms of skills and abilities, but also in terms of personality traits (e.g. self-belief, aggressiveness, etc.) of the passer, the receiver and their opponents. No single model could plausibly include all these and other factors and - we argue - this is not what modelers should pursue. As our brief review of model applications has highlighted, the models that bring the most interesting results are not necessarily the most complex, but those that are best tailored to the research questions

targeted and to identifying the variables needed to address them. Therefore, the challenge is not, or not only, to design bigger models with more variables, but models which can help us dig deeper in the subtleties of rich behavior and cognition, without necessarily achieving a high-fidelity representation of their real-world counterpart.

Furthermore, this review highlights that the landscape is still very scattered and most methods and models are developed on a case-by-case basis; a fact that has limited the application of the methods and reproducibility of results. This point becomes clearer if one considers that in many corners of cognitive science and neuroscience, there are not just standard cognitive paradigms (e.g., Posner task, Simon task) but also some standardized computational models that are able to account well for a relatively large set of laboratory designs. For example, in the field of decision-making, it is common to use standard computational models to address various kinds of forced choices between two options, with one or more attributes, regardless of the nature of the stimuli [125,224,225]. Doing the same in the context of ecologically valid behavior requires models that are tailored to its richness – which remain largely to be developed, let alone standardized.

5. Conclusions

Psychology and neuroscience are concerned with the study of behavior, of internal cognitive processes, and their neural foundations. However, these objectives have been long pursued by drastically limiting the range of behaviors that can be expressed, in order to make them easier to study in the lab. For example, perceptual and economic decision-making is typically studied in very restricted experimental settings, in which a person or an animal can make a limited number of choices (usually one of two button presses), presented in temporally separated trials, during which the choice offers remain static. In parallel, various influential computational models have been developed to formalize these settings, such the drift-diffusion model that addresses forced choices between two options, e.g., two button presses [125]. While reasonable, the above approach risks limiting our knowledge of brain and cognition – hence the present need to complement these with a more systematic study of ecologically valid behaviors.

The take-home message of this paper is that psychology and neuroscience are now in a good position to study rich and ecologically valid forms of behavior – and should increasingly pursue this opportunity. Indeed, we have recently witnessed a surge of novel methods and models – innovative experimental designs, measurement methods, and sophisticated computational models – that can facilitate the study of rich behavior. One example are sophisticated cognitive models that permit quantifying cognitive variables “in the wild”, such as the *surprise* associated with in-game events during basketball matches [177] or with the way a traffic situation will play out [7]. These new techniques and methods should be added to the toolbox of psychologists and neuroscientists, and complement classical techniques in order to extend the range of phenomena our disciplines can address.

Studying rich behavior requires facing many challenges, but perhaps the most crucial one is the development of sophisticated computational models able to capture the complexity of rich behavior and its relations with underlying cognitive and neuronal dynamics. This is why we focused our analysis on studies in psychology, neuroscience and other fields that have demonstrated the use of sophisticated computational models to successfully capture at least some aspects of rich, ecological behavior outside the laboratory. We hope that looking at these “success cases” can motivate psychologists and neuroscientists to study rich forms of behavior and the cognitive and neural processes that they engage.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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