Perspective

The Life of Behavior

Alex Gomez-Marin[1,*] and Asif A. Ghazanfar[2,3,*]
[1]Behavior of Organisms Laboratory, Instituto de Neurociencias CSIC-UMH, 03550 Alicante, Spain
[2]Princeton Neuroscience Institute, Princeton University, Princeton, NJ 08544, USA
[3]Departments of Psychology and Ecology & Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA
*Correspondence: agomezmarin@gmail.com (A.G.-M.), asifg@princeton.edu (A.A.G)
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Neuroscience needs behavior. However, it is daunting to render the behavior of organisms intelligible without suppressing most, if not all, references to life. When animals are treated as passive stimulus-response, disembodied and identical machines, the life of behavior perishes. Here, we distill three biological principles (materiality, agency, and historicity), spell out their consequences for the study of animal behavior, and illustrate them with various examples from the literature. We propose to put behavior back into context, with the brain in a species-typical body and with the animal's body situated in the world; stamp Newtonian time with nested ontogenetic and phylogenetic processes that give rise to individuals with their own histories; and supplement linear cause-and-effect chains and information processing with circular loops of purpose and meaning. We believe that conceiving behavior in these ways is imperative for neuroscience.

Living systems have self-sustaining properties that distinguish them from inert physical systems (Goldenfeld et al., 2017; Longo and Montévil, 2012; Maturana and Varela, 1987). They are typically composed of cells, maintain a stable internal state by converting food into usable energy, and grow and reproduce. Energy is acquired by the organism to keep its entropy low, defying for a time the inexorable march of the second law of thermodynamics. The morphology and physiology of living organisms facilitate their ability to acquire energy for sustenance. Constrained by morphology and physiology, another self-sustaining property of living systems is adaptive behavior. Behavioral strategies that improve an individual's ability to acquire energy and convert it to produce successful offspring ultimately help its lineage proliferate over evolutionary time through the process of natural selection (Pontzer, 2015). The latter is the ultimate goal of every animal (Darwin, 2004). This goal-directedness of animal behaviors is a feature that is absent in purely physical systems (Dawkins, 1976; Mayr, 1997; Wilson, 2000).

In the following, we put forth three essential principles for biological behavior. For each one, we will first provide its theoretical articulation followed by illustrative examples in the domain of behavior. The three principles are a subset of features arguably unique to life. We claim their necessity to understanding living organisms and reformulate them as fundamental principles in behavior rather than as mere characteristics. The principles are materiality, agency, and historicity. Behaviorally, they account for the constitutive roles of (1) morphology and environment; (2) action-perception closed loops and purpose; and (3) individuality and historical contingencies. These factors make up "the life of behavior." We hope that these considerations will shed light on our typical approach to understanding the mechanisms of behavior and why it is inadequate. We will elaborate upon each of these principles, but here is a summary of what to expect.

First, we often presume that the mechanisms of behavior will come more sharply into relief if the context in which the animal is placed is sterile (like a vat; e.g., fMRI scanner, Skinner box,

empty Petri dish, or monkey chair), the stimuli presented to the animal were simplistic and passively delivered (e.g., oriented lines, tone-pips, or tastants), and the body is considered simply as a container for the brain or the passive interface for the brain to control (the body as another vat). The presumption is that by doing so, many variables are controlled for and thus factored out, so that one can focus on just the neural or other physiological data being acquired (Figure 1A). However, there is no avoiding the fact that body and brain are inseparable in their function (Chiel and Beer, 1997; Tytell et al., 2011) and that they operate in a world that is unique to the organism under study (Thompson and Cosmelli, 2011; Von Uexküll, 1957) (Figures 1B and 1C). Second, we often take up the formulation that perception and action are the beginning and end of a linear process, a stimulus-response arc or "sensorimotor transformation" (Figure 1D). The organism, however, has goals (energetics, survival, and reproduction) and agency (it initiates actions rather than just responds to "irritations"). Its behavior is more akin to a control loop with inputs modifying outputs that in turn modify the next set of inputs, etc., to achieve a life-sustaining goal (Figures 1E and 1F). Finally, behaviors are variable. This is inconvenient to the scientist, but averaging across trials and groups of animals eschews the individual (Gallistel et al., 2004). Along the same lines, repeatedly presenting the same input signals in a temporally structured manner in order to repeatedly produce the same motor output obscures the fact that in the real world, no such thing could ever occur (Figure 1G). From the perspective of the animal, variable motor outputs are the means by which to achieve invariant perceptions that can satisfy the animal's goals (Bell, 2014; Powers, 1973). Specific goals are not static but vary in time, and each animal has a history on multiple timescales that determine its behavior (Figures 1H and 1I).

An Integrative Example: Tool Use by Chimpanzees

Chimps use sticks to gather honey, termites, and ants from the ground or trees in order to eat them without getting stung, bit, or pinched (Whiten et al., 1999). We can use this behavior to
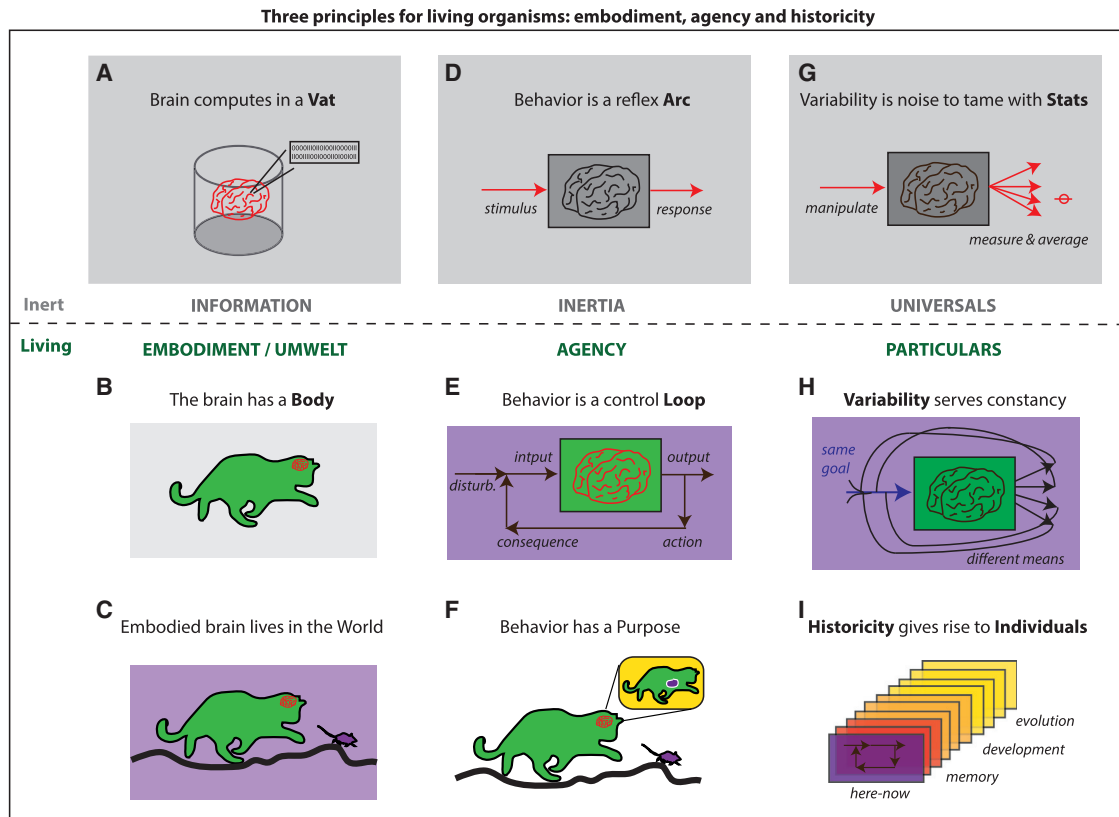
Three principles for living organisms: embodiment, agency and historicity

Figure 1. Accounting for the Life of Behavior
(A–I) What "vats," "arcs," and "stats" miss (top part), and three fundamental principles (bottom part) for the behavior of living organisms: materiality, agency, and historicity. Images in (A)–(C) concern embodiment and meaningful space, (D)–(F) deal with causality and real time, and (G)–(I) depict concrete history and individuality.
(A) Within the pervasive (and at times pernicious) information processing metaphor, life is nothing but information run in dull mater as disposable hardware.
(B) The brain is embodied, and the body is not a mere neural placeholder.
(C) The brain and its body live in the real world, under the constraints of physical surroundings (umgebung) but also in the meaningful environment of the animal (umwelt). In sum, materiality matters.
(D) Inertia is the default state of inert objects, whose motion is the result of reactive push-pull forces. Along with (A), brains are computers that transform stimuli into responses, which are equated with behavior.
(E) Beyond linear causality, a feedback loop goes through the world and back. Behavior then is not simple production of output but rather control of input.
(F) Servomechanisms fail to do justice to the fact that animals are proactive and have purposes in mind. Agency is intrinsic to life.
(G) Having de-contextualized space (A) and linearized time (D), the study of behavior falls prey to the "manipulate and measure" approach, where variability is deemed noise to be tamed with statistics.
(H) From the perspective of the animal, variable output serves to achieve intended invariant inputs. Living beings harness stochasticity.
(I) These iterative processes take place on multiple nested timescales, from actual genesis to ontogenesis to phylogenesis. Animals are individuals.

illustrate how materiality, agency, and historicity contribute to an explanation. The goal of tool-using in this case is to acquire energy. This goal belongs to a hierarchy of goals: a higher level than having enough energy is the goal of not dying; a level below acquiring energy is the goal of finding a tool and then using it properly, which in turn entails the goal of approaching the potential food source. Levels above answer why; the levels below answer how. Depending on the task (breaking, prodding, or collecting), the stick can be held in various ways, including the precision grip (that is, between any two fingers but without the use of the palm). This illustrates an equifinality; chimps will diverge in the means but converge in the goal. To perform a precision grip requires specific hand biomechanics (e.g., thumbs that rotate around a joint; Napier and Napier, 1985). All Old World primates (and one New World monkey) can perform a precision

grip; other animals cannot. Tool use also requires specialized neural circuitry operating in conjunction with those biomechanics in a goal-directed manner. The precision grip is correlated with extensive cortico-motoneuronal terminations in the ventral horn of the spinal cord (Bortoff and Strick, 1993; Lemon and Griffiths, 2005), and motor planning and coordination are associated with neocortical areas 2 and 5, which are enlarged in tool-using primates (Padberg et al., 2005). Finally, tool use is also a learned behavior; young chimpanzees learn by watching older chimpanzees combined with trial and error (Tomasello et al., 1987). Thus, tool use is a behavior bound to the body and brain circuits, and that emerges on evolutionary and developmental timescales.

In the analysis of tool-use behavior, the body and the environment cannot be added later. They may be literally peripheral, but

not conceptually. The behavior only emerges because of the organism's worldly and bodily activities. In terms of the world, for example, chimpanzee populations exhibit differences in ant foraging, as tree branches usable as tools for gathering ants are present at some sites, but not in others (Whiten et al., 1999). Even the species of ants can influence tool use (Möbius et al., 2008; Schöning et al., 2008); more aggressive ant species, for instance, necessitate longer tools by chimpanzees to avert biting of their hands (Humle, 2011). In light of all this exquisitely rich evidence about the myriad of spatial and temporal dimensions that constitute tool use by chimps, one may wonder to what extent a purely neural explanation of such behavior—one that would successfully map its circuitry completely and exhaustively dissect all the so-called necessary and sufficient neurons involved (something not too far, it seems, from the neuroscientist's dream; Dawkins 1976)—could become an explanation of the behavior (Krakauer et al., 2017).

Now, we will elaborate upon each of the three principles of life as they relate to behavior.

Part I - Materiality: Brains Have an Embodied Life in the Real World

Natural behaviors are inescapably contingent on context (space) and history (time). The "space" for any animal is its body and environment. This context is explanatorily inseparable from the content; it is always constitutive of the behavioral phenomenon itself. Attempting to control the space by placing animal (Skinner box, restraint chair, or using an "anesthetized" preparation) or human (e.g., fMRI scanner) in an "impoverished" arena while delivering isolated, reduced, and/or arbitrary sensory signals to elicit stereotyped bodily actions is effectively attempting to create a vat in which it is presumed that greater understanding of the brain and behavior will emerge. On the contrary, it is more like attempting to do the brain's job for it. The brain has a body that evolved and developed together as a unit embedded in the world (Figure 1A).

The Brain-Body

We typically treat the body as if it is simply the carrier of the brain, with the brain being the central computing device for processing unfiltered inputs from the outside to generate platonic forms of motor outputs. What we forget is that the body, and its species-typical structure, is constitutive in this process. Different parts of the body act as filters for both incoming and outgoing signals (Chiel and Beer, 1997; Tytell et al., 2011). Thus, the way we interact with the environment—the way we acquire sensorimotor knowledge—is in inextricably dependent upon the shape of our bodies (Noë, 2004). Animals with differently shaped bodies interact with the world differently and thus acquire behavioral capacities in different ways. This is not just about differences, however; without a body, behavior and cognition are impossible (Brooks, 1991).

Every part of a species' anatomy potentially exhibits both species-specific specializations and individually specific variation. The outer ear, for instance, is extremely variable in size, shape, and mobility, even among primates, and these factors determine how one hears (Fleagle, 2013). In nocturnal primates that rely primarily on hearing to catch prey, the ears are very large (relative to head size) and mobile. Mobility is conferred through a special set

of muscles. In humans, the ear is small and does not move very much. The shape of the ear—its ridges and valleys—filter sounds before they hit the eardrum (Batteau, 1967). Critically, which parts of a given sound get louder or softer according to this filtering also depend on whether the sound is hitting the outer ear from above or below. Through learning, we learn to associate those acoustic differences with the vertical location of the sound source.

The constitutive role of our bodies' physical conformation to behavior and experience is reflected in how it changes and guides the nervous system during development. Continuing with the ear example, we localize sounds well at a very young age, but since our ears are still growing and changing shape, the developing brain must recalibrate itself to account for these bodily changes (King and Moore, 1991). Contrary to what one would assume, the neural circuits of the auditory system are dependent upon the shape of the ears to guide their function. Auditory cortical neurons in very young ferrets encode spatial location poorly (Mrsic-Flogel et al., 2003). The standard presumption to explain this poor tuning would be that the neural circuits are still developing (e.g., perhaps lacking refined inhibitory inputs) and/or need to time to be molded by experience. However, the coarse spatial tuning is actually because the shape of the ears (the body) is still developing and not yet adult-like. Experimentally providing the same young ferrets the ears of an adult (via virtual acoustics) can immediately drive those auditory cortical neurons to encode sound location with adult-like accuracy (Mrsic-Flogel et al., 2003). Thus, the developing body is guiding the sensory functions of the nervous system in this case, not the other way around.

The developing body also shapes motor output. Human newborns, for instance, are able to make well-coordinated stepping movements when held upright, but these movements disappear by the time they reach ∼2 months of age (Thelen et al., 1984). While it was assumed by many that the change in stepping behavior was due solely to the developing nervous system (e.g., the behavior disappeared because there was too much inhibition that had not been "pruned" back yet; McGraw, 1945), Thelen et al. (1984) hypothesized that the loss of stepping behavior was due to body growth; the infants' legs typically fatten up postnatally, and they do not yet have the strength to move heavier legs. To test this hypothesis, they submerged the infants' legs in water, effectively decreasing their mass. This resulted in the reappearance of stepping and thus falsified the alternative hypothesis that neural change was necessary. The change in behavior was due to changes in the body.

Along similar lines, it would typically (and reasonably) be presumed that changes in vocal production over the course of development are the results of learning and, thus, changes in the nervous system. In growing marmoset monkeys, however, computational modeling and experiments placing infants in helium-oxygen environments revealed that, as lungs grow bigger, their changing sensory feedback onto vocal central pattern generators results in the disappearance of the production of context-inappropriate vocalizations without any need for concomitant changes in CNS structure (Zhang and Ghazanfar, 2018). The developing body can create distinct behavioral changes by itself and reduce the computational and energetic

burden on the nervous system (a strategy that is often exploited by roboticists; Pfeifer et al., 2007).

The Body-World

All animals share a common world, but not all animals have a world in common. Each organism has its own umwelt (meaningful environment) and not just an umgebung (physical surroundings) (Von Uexküll, 1957). The umwelt is a foundational concept in zoology, with theoretical implications for neuroscience's anthropomorphism (Gomez-Marin, 2019). Every animal species (and, within it, every individual) experiences the world differently. The world, considered as a physical fact, is the objective space in which we observe animals behave. As a biological fact, however, the relation between organism and environment is such that the former not only submits to the latter but actually carves it out. For psychologists, the Gibsonian translation is "affordance." It means, for example, that a stone is not simply a stone but a-stone-for-a-snail as an opportunity to climb or a-stone-for-a-human as an opportunity to throw and hit something far away.

As scientists, no doubt, we can act on an organism. Umwelts (or umwelten, in proper German) are not just parallel universes, they intersect; cut a tree, and the birds must leave. Yet, the physical excitation we present to animals as part of our standard experimental designs not only needs to occur but also has to be noticed. What the organism cares about is what it will attend to, thus dictating its perceptions (and the actions, by virtue of which it will manage those perceptions). In other words, the umwelt is "an elective extraction from the Umgebung" (Canguilhem, 2008, p. 112). Paradoxically, in the typical behavioral or neuroscience experiment, the umgebung (which is alien to the animal) is in turn nothing other than the umwelt of the scientist (scientists are humans, and humans are also animals), who are operating in the symbolic universe of abstractions (coding, entropy, statistical significance, etc.). The umwelt thus reveals a strong and concealed "conflict of interests" in biology. If behavior is a functional loop that is enacted in a meaningful context, then animals (the objects of study of the scientist) are also subjects (studied by other subjects: us). This creates what could be called a "clash of umwelts." The almost uncountable variety of worlds—all seemingly as far away from each other that they become almost nonoverlapping, even incommunicable (Calvo, 2017; Nagel, 1974)—are actually in conflict with one another. What is meaningful from the point of view of the organism need not be from the point of view of the scientist studying it, and vice versa. As Canguilhem (2008) puts it, "Hedgehogs as such do not cross roads….On the contrary, it is man-made roads that cross the hedgehog's milieu"(p. 22).

The biology of animals thus poses a conundrum to the object-subject separation that allowed so much progress in physics in particular and science in general. The underlying mission of physics is to establish laws between objects that are valid regardless of the point of reference, which implies and necessitates the absence of any absolute center. Yet, biology is a historical science whose objects of study are individuals. To be objective would then entail to decenter oneself (the scientist) while keeping the organism at the center. We neuroscientists, rightly concerned with anthropomorphism in our interpretations, should revisit the notion of objectivity in favor of zoomorphism: to study animal behavior from the perspective of the animal. This, of course, has immediate practical consequences for the design of our experiments. The use of artificial, "simplified" stimuli in behavioral and neural experimentation is commonplace (oriented lines, tones, moving dots, etc.) (Hauber et al., 2015; Rust and Movshon, 2005), but every choice made by us with our own goals in mind is making assumptions about the perception and goals of the animal under study. A paradigmatic example is when a scientist says that no stimuli were presented to the animal (an approach that seeks to control or limit sensory experience), whereas any human prisoner in isolation knows that there can hardly be a bigger perceptual experience than that.

Lahti (2015) dubbed these assumptions about what an animal may or may not care about as the "umwelt gamble." By gambling, one ignores the fact that animals are biased toward certain modalities and signals within them and may interpret such signals in a way an experimenter cannot guess at. Even the manner in which we mark individuals for purely identification purposes (e.g., collars, tags, dyes, bands) can influence behavioral patterns that we may think are isolated only to the experimental variables of our own choose. For example, a study in which male zebra finch were individually identified through the use of colored leg bands (a widely used practice) unexpectedly found that those leg bands influenced female choice (Burley et al., 1982). Similar unexpected influences of colors occur in humans as well. Across a range of sports, wearing red is consistently associated with a higher probability of winning, indicating that we respond to different colors differently without even realizing it (Hill and Barton, 2005). It is thus more appropriate to conceive the world as a forum for action than as a place of things.

Umwelts are unique not only to species but also to individuals. How you engage with the world is different from how others do, and this difference, of course, can be related to an individual's body in nontrivial ways. For example, in both the visual and auditory domains, objects with a looming motion toward an observer (i.e., are rapidly approaching versus receding) have a perceptual priority. When observers are asked to estimate the arrival of looming sound sources, for instance, they consistently respond too early, perceiving them as closer than they actually are (Rosenblum et al., 1987). In a natural environment, this underestimation results in more time to act—to evade or engage the source—and thus affords a "margin of safety" that may provide a selective advantage (Neuhoff et al., 2012). This idea is consistent with comparative work on the perceptual biases toward looming sounds (Ghazanfar et al., 2002; Maier et al., 2004) and with neuroimaging data showing that looming sounds preferentially activate motor planning areas (Seifritz et al., 2002). However, perceiving and acting in response to looming sounds depend not only on perceptual abilities and the neural activity it elicits but also on the motor capabilities of the listener. Listeners with less physical strength and lower aerobic fitness respond sooner to looming sounds and with a larger margin of safety than listeners in better health (Neuhoff et al., 2012). This shows that, within a species, the umwelt and the individual body form a system that enables adaptive behavior.

Note that like the world itself, the individual body changes over time and, as a result, so does an individual's umwelt and the behavior exhibited. In human infancy, for example, there are changes in the ways the body moves in, and interacts with, the
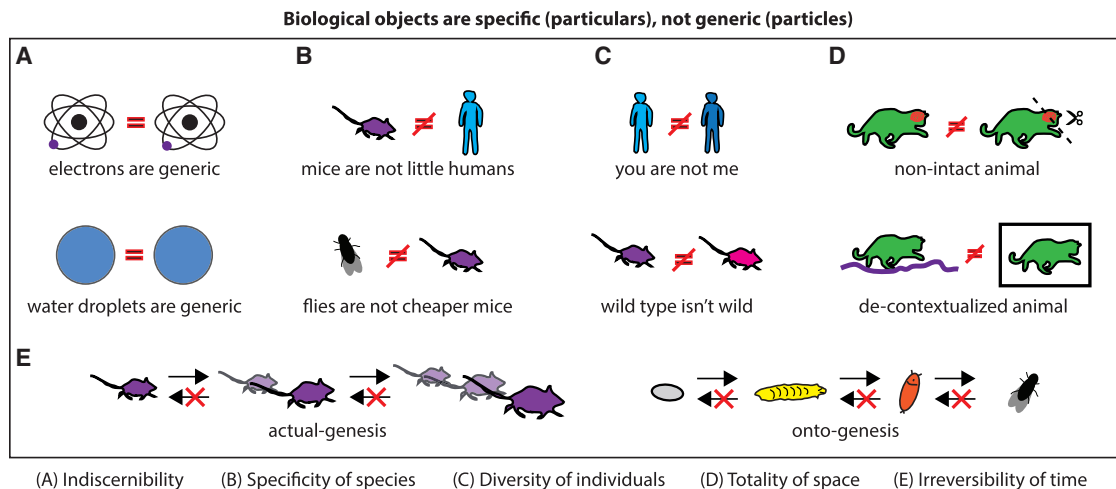
Biological objects are specific (particulars), not generic (particles)

| (A) Indiscernibility | (B) Specificity of species | (C) Diversity of individuals | (D) Totality of space | (E) Irreversibility of time |

Figure 2. There Is No *Ceteris Paribus* in Experimental Behavioral Biology
The principle "the same produces the same" is inapplicable in experimental biology, since the covert assumption "all things being equal" actually fails.
(A) Inert systems can be treated as indistinguishable—they have no history, agency, or personality.
(B) Despite the existence of common biological mechanisms and shared principles of behavior, humans are not a collage of a handful of laboratory animals. Organisms with fewer neurons are not necessarily "simpler" organisms either, and "organism models" are not "model organisms" (Katz, 2016).
(C) Laboratory wild-type animals are often anything but wild or exact controls for transgenic animals. Average group behavior may not coincide with any of the behavior of the individuals in that group. Individuality is real and relevant.
(D) Behavior studied in animals whose bodies and worlds have been truncated can be misleading and not generalizable (the behavior of a paralytic cat in an empty arena is far from cat behavior).
(E) During development, animals undergo major changes not only in their behavior but also in their bodies. Despite our sequential measurements, behavior is generated serially. History matters.

environment (e.g., sitting up to crawling to walking). These changes, in turn, impact the development of skills and experiences that play a role in the emergence of other behaviors such communication (Iverson, 2010). Learning to sit upright without support allows deeper breathing that increases the power for producing longer, less noisy vocalizations like babbling (consonant-vowel combinations) (Iverson, 2010). The production of babbling results in more frequent contingent responses from caregivers (Gros-Louis et al., 2006), which acts as a ratchet for further vocal learning by the infant (Goldstein and Schwade, 2008), thus leading to new forms of communication with increasing complexity. An infant that can sit up has also changed the way she observes the world and engages with caregivers (e.g., joint attention), as the infant can now freely rotate the head and trunk. Moreover, the hands are more able to grasp and manipulate objects, providing greater opportunities to share with caregivers who, in turn, facilitate further communicative development (e.g., by naming objects held by infants) (Iverson, 2010). In these scenarios, caregivers (part of the umwelt) adjust to the infant's changing behavior. The developing body and motor skill acquisition results in an ever-changing meaningful environment.

Part II - Agency: Behavior Is Not an Arc but a Loop in Service of a Goal

It may seem like a truism to claim that behavior is the ultimate output of the nervous system. Although it is difficult to define what constitutes behavior (Levitis et al., 2009), most would argue that it is some sort of output. Having access to the neural level does not modify this position (Gomez-Marin, 2017). Even Tinber-

gen (1951), one of the founders of ethology, defined behaviors as the "total movements made by the intact animal." Typically, this end product is considered the result of a sensory-motor transformation. Behavior in the form of this arc then allows the experimenter to vary the sensory inputs (manipulate) and observe the motor output (measure) to estimate a "transfer function" of behavior, followed by an investigation of the neural mechanisms that may be the implementation this computation (Calhoun and Murthy, 2017).

A first caveat with this methodological "manipulate and measure" ideology is the inapplicability of the assumption of *ceteris paribus* ("all else being equal"). We set up our experiments and interpret the data under the scruple that the results are valid under that assumption. But there is no *ceteris paribus* in biology (Figure 2). This means we cannot copy and paste the conceptual presuppositions and experimental approaches we use in physics (Figure 2A). Experimentation in behavior needs to account for (1) the specificity of different animal forms across species (Figure 2B); (2) the diversity of individuals within species (Figure 2C); (3) the totality of the organism and its environment (Figure 2D); and (4) the irreversibility of lived experience (Figure 2E). We will come back to some of these points later.

There is a second related conceptual caveat to the behavioral arc: once the animal is engaged, the supposedly independent variable (sensory input) is not independent anymore; the output feeds back and, together with the stimulus, constitutes the input to the organism, producing the output again. Thus, behavior is not linearly causal as the sensory-motor transformation idea implies. The motor response influences the subsequent sensory input, and the sensory input determines the motor response.

Behavior is a loop, not an arc. Or as Dewey (1896) wrote more than 120 years ago, "What we have is a circuit, not an arc or broken segment of a circle." The so-called readout, conceived as the result of the operations of the brain matter upon something we experimenters "write in," reflects a covert anthropomorphism; what the animal does is what we see, and what it sees is what we do. Behavior is something more than this linear sensory-motor transformation inscribed in a stimulus-response phenomenon. It is circularly causal, consistent with the cybernetics idea put forth by Wiener (1949) and later advocated by others (e.g., Ahissar and Assa, 2016; Churchland et al., 1994; Powers, 1973). Behavior is, to a great extent, the control of perception (Powers, 1973). Namely, living beings have life-sustaining intentions (fleeing, fighting, feeding, and reproducing), and they behave in order to satisfy them. Perceiving the consequences of their actions is the only way they can know, and so it is actually the only thing animals care about. In other words, for an animal, its output means little if it does not control, in some way, its input.

The essence of the problem thus stems from a simple but subtle confusion, a conflation of space with time. What comes in (which certainly must be called input) is not what comes first (the so-called stimulus), nor does what comes out (output) constitute what is last (response). The notion of stimulus implicitly postulates the beginning of the whole situation, which is only so from the experimenter's point of view. Here are examples of behaviors cast in the light of behavior loops instead of arcs.

Robbing and Dodging Rats

Social interactions are often considered as complex behaviors requiring complex mechanisms, and as social group size increases, it is typically believed that greater amounts of neural resources must be dedicated to such behaviors (Dunbar, 1998) (though the validity of these ideas has been increasing called into question; see Barrett et al., 2007; DeCasien et al., 2017; González-Forero and Gardner, 2018). Cybernetic approaches to social interactions reveal that seemingly complex behaviors can arise through simple rules and thus do not require increasing amounts of computational power (Barrett et al., 2007; Pellis and Bell, 2011). For example, rats are social animals, and one consequence of that is that they must protect their food from other rats that want to steal it. Robbing and dodging in rats involves one animal (the dodger) possessing a small piece of food and another animal (the robber) attempting to acquire the food (Bell and Pellis, 2011; Whishaw, 1988). The robber approaches the head of the dodger, and the dodger evades by swerving laterally away. Given the apparent correlation between the angle swept through by the dodger to evade the robber and both the type of food being consumed and the identity of the robber, this food-protection behavior seems to be an excellent system in which to study a complex, ethologically relevant aspect of rat social cognition. In this view, the dodging rat must calculate the angular displacement of their swerve away from the robber, calculate the time it takes to eat a piece of food, and take into account the robber's identity, distance, and speed. This seems like exceedingly complex cognition given that rats make dodging decisions and movements in fractions of a second and most often do so successfully. Because we are fascinated (as one should be) by the complexity of the brain,

we have no difficulties in ascribing really difficult computations to it.

An alternative hypothesis—a closed-loop hypothesis—is that the dodger's goal in such a context is simply to maintain a constant distance from the robber (Bell and Pellis, 2011). Any behavioral change with regard to food type or eating time could be accomplished by simply decreasing or increasing the inter-animal distance. Such a rule would eliminate the need to perform complex and time-consuming computations by only considering the maintenance of a constant distance between two animals, as opposed to the calculation of a dodge angle based on more elaborate information. If this closed-loop hypothesis is correct, then dodger angle should be a compensatory action in order to maintain the controlled variable (inter-animal distance). In light of this hypothesis, a new analysis of food-protection behavior revealed that the dodger moved to maintain a set distance from the robber (regardless of the robber's movements) and that the distance was far less variable than dodger angle (Bell and Pellis, 2011). Moreover, context cues such as food type and the identity of the robber had the simple effect of increasing or decreasing the inter-animal distance that needed to be achieved by the dodging rat. (For a highly quantitative study illuminating how motor variability serves perceptual constancy in the domain of touch, see Saraf-Sinik et al., 2015.)

Vocal Turn-Taking in Marmoset Monkeys

Here is another example where seemingly complex behaviors are accounted for by simple closed-loop heuristics. One way to enhance signal quality during communication is to prevent interference through taking turns. By pausing after transmission, a sender allows signals from other individuals to transpire and be heard before another signal is emitted. The elimination of overlap via turn-taking increases the likelihood of the signal being heard accurately. As a consequence, an exchange of signals between two or more individuals has a structure. A successful instance of human vocal turn-taking, for example, would involve person 1 speaking while person 2 attends, followed by a response from person 2, be it a statement or an indication for person 1 to continue speaking. These rules are universal for human conversations (Stivers et al., 2009). It has been argued that this human cooperative vocal communication is unique and requires complex cognitive traits like mind reading (shared intentionality) not observed in other primate species (Tomasello, 2008).

An alternative hypothesis is that vocal turn-taking (particularly, in nonhuman primates) is a closed-loop behavior with the goal of maintaining social contact (a form of "grooming at a distance"; Kulahci et al., 2015). A study of the vocal exchanges of a small New World primate, the marmoset monkey (*Callithrix jacchus*), showed that they will participate in contact call exchanges with any conspecific and that these exchanges have a temporal structure that is similar to the turn-taking rules that humans use (Stivers et al., 2009; Takahashi et al., 2013): rare interruptions and a consistent silent interval between utterances. However, there is no evidence that marmosets have any mind-reading skills like humans. Evidence that humans engaged in turn-taking are in a closed loop includes that there is (1) periodic coupling in the timing of utterances across two interacting individuals and (2) entrainment, where if the timing of one individual's vocal output quickens or slows, the other's follows suit (Chapple, 1970;

Oullier et al., 2008; Schmidt and Morr, 2010). The vocal exchanges of marmoset monkeys share both of these features (Takahashi et al., 2013).

Consistent with the idea that turn-taking is driven by the goal of social contact, humans adjust the amplitude of their voices as a function of distance from a listener; we do so in a manner that would compensate for such distance (Pelegrín-García et al., 2011). Again, this ability is presumed to be the product of high-level sociocognitive skills, like theory of mind. Non-human primates like marmoset monkeys were thought to lack such socially related flexibility in vocal production. However, based on the predictions from a simple model whereby vocal feedback from a conspecific modulates the drive to produce a vocalization (Takahashi et al., 2012), it was hypothesized that they should readily be able to exhibits this type of cooperative vocal control. A playback experiment revealed that marmoset monkeys, like humans, increased the amplitude of their contact calls—and produced such calls with shorter response latencies—toward more distant conspecifics (Choi et al., 2015). Cooperative vocal control appears to be a simple system property with the goal of social contact that does not necessitate any particularly advanced sociocognitive computations.

It is important to note that just closed loops are not sufficient. For example, Braitenberg (1986) vehicles are passive-reactive machines with simple circuits in a closed loop with signals in the environment that, via our reflexive anthropomorphism, seem like they have goals and desires but obviously do not. Exquisite mimesis does not qualify as living (Rosen, 2000). Real biological organisms, from bacteria to giraffes, need to move forward in the world. Moving, in turn, implies decision making: to move there and not here. Perception can be conceptualized as closed-loop convergence processes (Ahissar and Assa, 2016). One needs to decide what to look at, and to see, one needs to look. The study of behavior must then confer proactivity and subjectivity to their objects of study as well as real purpose. This is possible by erecting a principle extending the physical principle of inertia: agency. The inertial view of nature applied to living beings reads that things do not change by themselves; one must push them so that they push back. This assumes (whether intentionally or not) that behavior operates via a passive mechanism. But animals are agents capable of producing actions, not just responses. They are proactive, not reactive.

Part III - Historicity: Living Organisms Are Individuals
Behavioral variability is always deemed as noise to a first approximation (Figure 1G). This reflects our drive to go from concrete instances to universal claims. The standard is to reproduce and replicate. Yet, the relatively neat assumption that "everything else is being kept equal" becomes particularly problematic for behavior, because every moment of behavior is the result of a unique history, a history that has unfolded on many different timescales. In physics, we often seek atemporal relationships among universals (rather than particulars) and perceive that what is of real importance is to be found in general laws and normative explanations of behavior. But what if behavioral variability is not an inescapable "bug" of biology that scientists must contend with but an adaptive feature? Variability is perhaps the ability to vary rather than the "nausea" (noise, etymologically)

of the scientist not being able to make sense of the system. Earlier, we argued that motor variability serves perceptual constancy (and not the other way around). A strong corollary of the principle of historicity is twofold: the lack of (1) genericity in biological objects (two electrons are interchangeable, but two homozygotic twins are not) and (2) specificity of biological trajectories (Longo and Montévil, 2012). Like the different spatial scales of the umwelt, biological historicity plays out on different nested timescales, and the variability that is generated from an individual's history writ large seems more functional than noisy.

In fact, methodological approaches that specifically try to reduce or eliminate phenotypic variability are disappointing when considered carefully. For example, much of neuroscience uses inbred strains of mice housed in uniform environments. The motivation behind this is based on the notion that there are genetic mechanisms that should yield the persistence of certain phenotypes in the face of environmental factors that cannot be controlled for (revisit Figure 2). However, this turns out to be impossible. When the spontaneous homecage behavior of commonly used inbred mice, raised under identical conditions, was measured using automated procedures, there was substantial variability (Loos et al., 2015). Moreover, across different strains of inbred mice, there were different levels of variability; some strains were much higher in their behavior variability than others. This is important, because one might have suggested that the within-strain variability was just unaccounted-for environmental factors or related to the stochastic effects of physical laws at the molecular level (e.g., intermolecular interactions subjected to thermodynamic instability) (Honegger and de Bivort, 2018), but this would not explain systematic across-strain differences. In fact, it suggests that behavioral variability is built into the system. In support of this, a study of inbred lines of *Drosophila* was used to address the variability of locomotor "handedness" (the tendency to turn left or right in a y-maze) (Ayroles et al., 2015). Like the mice strains, there was considerable variability in the trait, and the amount of variability was linked to different genotypes. By crossing flies with measured levels of handedness variability, the degree of variability was shown to be heritable. Even behaviors that appear as reflexes show heritable variability, such as the startle response in zebrafish (Pantoja et al., 2016) or in the parthenogenetic pea aphid whose clonal daughters show variation in leaping-from versus clinging-to vegetation (Schuett et al., 2011).

These data show that evolution has not selected out the mechanisms that generate behavioral variability (and thus, individuality); rather, it has selected for them. Behavioral variability is advantageous, because the environment is unpredictable, and thus an individual's umwelt may not be exactly the same as its parents' umwelt. Built-in behavior variability ensures that at least some individuals may be able to thrive under a novel set of conditions—a form of bet hedging (Honegger and de Bivort, 2018).

Behavior and its neurobiology are the product of not only evolutionary processes but also developmental ones as well (Gould, 1977). Evolution acts on developmental processes to produce adult phenotypes. Changing developmental trajectories is the only way to evolve phenotypic changes. More pointedly, adaptive behaviors that are learned initially can drive the evolution of developmental processes that include the modification

of genes. For example, if the goals of any organism (reproduction and survival) were enhanced by a new behavior acquired through learning, then the differential survival of those individuals might be enhanced by skipping the time it takes for the learning to occur by assimilating the process during development. This is known as the Baldwin effect (Baldwin, 1896). For example, human populations with a tradition of raising domesticated animals for milk production have acquired lactose tolerance via the evolution of developmental changes (including genetic changes) that keep the lactase enzyme active during adulthood (Laland et al., 2010). Dairy culture increases the selective advantage for this trait.

In contrast, some features of a meaningful world change rapidly or encompass a broad range. In those cases, it is most adaptive for every individual to retain some form of development plasticity as opposed to evolving a built-in mechanism. Human infants, for example, show perceptual abilities that are broadly tuned, but as development proceeds, these abilities become narrower in scope as a function of experience (Lewkowicz and Ghazanfar, 2009). In the domain of speech, young infants can discriminate between native and nonnative phonetic contrasts, but older infants can only discriminate between contrasts that are present in their native language. Six- to eight-month-old English-learning infants can discriminate nonnative consonants, such as the Hindi retroflex /Da/ and the dental /da/, but 10-to 12-month-old infants cannot (Werker and Tees, 1984). The general decline in the salience of nonnative phonetic contrasts is due to language-specific experience (Kuhl et al., 2003). A similar perceptual narrowing occurs for face, music, and multisensory perception (Lewkowicz and Ghazanfar, 2009). There are, of course, neural correlates of experience-dependent behavioral development (e.g., Gomez et al., 2017), including the emergence of brain regions that are driven purely by culture (e.g., literacy; Dehaene et al., 2010). Thus, bet hedging for robustness against changing environments can take the form of built-in variability (genetics as in fly handedness described above) and/or phenotypic plasticity (such as experience-dependent behavioral plasticity) (Honegger and de Bivort, 2018). Both phenomena operate on two timescales—species evolution and individual development—and are of a piece. For example, the increased behavioral and neural plasticity that humans exhibit relative to other primates is via evolutionary changes in gene expression that allow us to retain neural plasticity for a much longer period during a lifetime (Bufill et al., 2011; Somel et al., 2009).

Learning, plasticity and other responses to a changing environment are not restricted to developmental period. The history of behavior in real time counts as well. One can distinguish between phylogenesis, ontogenesis, and actual genesis (Gomez-Marin et al., 2016). Every behavior carries with it not only the dynamics of the immediate performance but also a momentum (i.e., hysteresis) (Hock et al., 1993). This real-time history is unaccounted for in most approaches to measuring behavior, where the start of a new measurement period is considered an isolated event. Typically, as the subject (human or animal) performs for a duration of time, no account for even basic phenomena such as body condition, fatigue, or levels of satiety are considered. The implicit assumption is that they do not matter. As a result, we develop mistaken ideas about the underlying mechanisms. Although hysteresis effects are seen in perception (e.g., speech categorization; Tuller et al., 1994), it's most directly apparent in motor behavior. For example, in the A-not-B task, infants watch an experimenter hide an object in one location, A (Piaget, 1954). They are typically allowed to search for the object after a short delay, and this procedure is repeated some number of times. Infants then watch the experimenter hide the object in a new location, B. After this switch, infants often search perseveratively at A. Many cognitive and neural-based accounts were developed to explain this phenomenon, including deficits in object representations, working memory, and response inhibition as a result of immature prefrontal cortical development (Diamond and Goldman-Rakic, 1989). However, it turns out that the infant's perseverative reaching to A on B trials is the result of their history of reaching to A; the likelihood of reaching to A on the B trials is an increasing function of the number of past reaches to A (Smith et al., 1999). Hysteresis, of course, also accounts for the aftereffects observed following sensorimotor adaptation in reaching (Von Helmholtz, 1867) and speaking (Houde and Jordan, 1998). Even fundamental behavioral measures such as reaction times, typically thought to reflect the speed of computing decisions and preparing actions, are subject to history effects. Prior experience in one visuomotor task can speed up the reaction times in another task requiring a different movement strategy (Wong et al., 2017). Thus, reaction time is influenced by prior experience, and standard neural accounts of reaction time must be reconsidered.

Individual behaviors carry with them a history and build momentum; these accumulated histories constitute the stuff of learning and development change. Learning and developmental change can lead to differential engagement with the environment, a new umwelt that in turn affects individual behaviors. "Habit, memory, learning, adaptation, and development form one seamless web built on process over time—activities in the real world" (Thelen and Smith, 1998). The organism (brain and body) changes over time (evolution, development, and single event), which changes its umwelt (niche and affordances), which then modifies the organism (brain and body). It is perpetual change in a closed loop, rolling toward a goal (survival and reproduction) while also unfolding, rather than unfurling, creatively (Bergson, 1907).

Every individual mouse, fly, monkey, and human has a history that forges its behavior.

Summary

In Figure 1, we summarized three principles alien to inert behavior that we think characterize the life of behavior: materiality (an embodied brain embedded in the world), agency (circular causality with the capacity to initiate actions in order to attain particular purposes), and historicity (individuality and individuation at multiple timescales). In Figure 2, we emphasized the inapplicability of a basic principle of scientific experimentation: the assumption of restoration of initial conditions, the "all else being equal" idea. Animals are particulars, not particles. These entail special difficulties to the biological object of study. Let us revisit those claims.
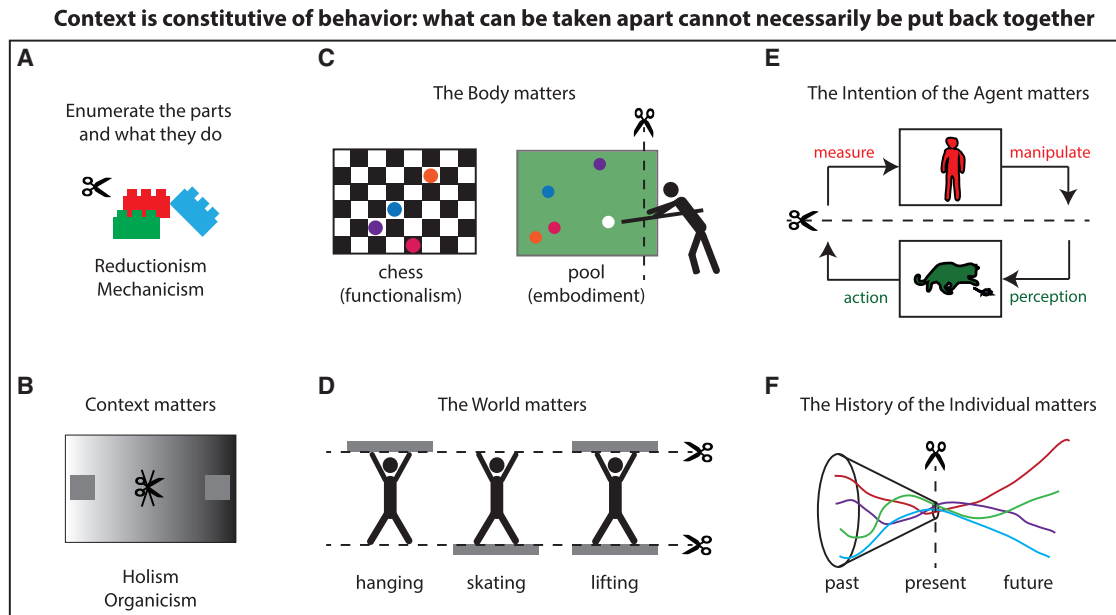
Context is constitutive of behavior: what can be taken apart cannot necessarily be put back together

Figure 3. Beyond a Frankenstein Biology
(A) The modern approach to understand behavior "cuts" but fails to "stitch." Wholes are taken to be the sum of their parts, which in turn are considered replaceable. Context is believed to be dispensable. Biology literally becomes puzzle-solving; like in a Sudoku, our job is to fill in the gaps or crack the circuit.
(B) In opposition to (A), after cutting, one cannot really sew life back the life of behavior, because context is constitutive and thus inseparable from content. This tension is illustrated in (C) and (D) with respect to space and in (E) and (F) with respect to time.
(C) Do not cut the body, as it is not a neural "plug-in" for behavior. For instance, in chess, only algorithm matters, and implementation is irrelevant. The hardware-software split (a form of crypto-dualism) easily endorses a pseudo-materialism (indifference to matter). However, in pool, the body is an inextricable part of the game. One can never play the same pool game twice.
(D) Do not cut the world. Even when the body is taken into account, the same posture can reflect very different behaviors. Leaving the world out literally leaves the body floating in an empty space, disregarding the umwelt of the animal. The meaning of the behavior is then lost.
(E) Do not cut the loop. When our study of the organism in the lab is framed under the "manipulate and measure" arc, anthropomorphism has crept into the interpretation of behavior before any data are even collected. The organism, being an agent like the scientist, is also trying to measure and manipulate. Thus, linear causality (so dear to us) is a broken loop that cannot account for the circularity that constitutes the behavior of organisms.
(F) Do not cut the history. The restoration of initial conditions is an abstraction inapplicable in biology. Living organisms are individuals; they have their own history. Treating them as indistinguishable particles smears out their intrinsic differences and trumps not only predictability but biological understanding.

Part I

We neuroscientists have no problem acknowledging that brains need bodies only to indefinitely postpone adding them to our mechanistic framework. The same is true with bodies embedded in the world. This is our main bias; we believe that the "real deal" is taking place inside the skull and that all the rest is an add-on. As a result, our typical approach is to remove context (body, or umwelt) in order to distill content (information or algorithm) to then be able to predict the behavior in any context. A subtle philosophical distinction lies at the bottom of this: whether non-neural stuff facilitates or constitutes behavior. We hope we have convinced you that their role is constitutive. Materiality does not mean dull matter as a principle of the life of behavior; rather, it is the recognition of the meaningful-lived world of the flesh.

Part II

In stressing that animals operate under circular causality, one could be tempted to conclude that what we need to do is to map animals to machines. Behavior would then be an engineering problem. Such a view would not grant animals with purpose, however. The life of behavior is circular causality toward a goal. William James made the distinction beautifully: "If now we pass from such actions as these to those of living things, we notice a

striking difference. Romeo wants Juliet as the filings want the magnet; and if no obstacles intervene he moves towards her by as straight a line as they. But Romeo and Juliet, if a wall be built between them, do not remain idiotically pressing their faces against its opposite sides like the magnet and the filings with the card. Romeo soon finds a circuitous way, by scaling the wall or otherwise, of touching Juliet's lips directly. With the filings the path is fixed; whether it reaches the end depends on accidents. With the lover it is the end which is fixed, the path may be modified indefinitely" (James, 1890, p.7). For the behavior of animals, the principle of inertia (and stimulus-response) should be rejected in favor of agency, generalizing "descent with modification" of species to individuals (Soto et al., 2016) and at all temporal scales. Finally, with respect to causality, there is an irresistible tendency by us to anthropomorphize it in the flavor of linear causality, namely, counterfactuals (Gomez-Marin, 2017). We tend to posit that the essence of behaving entails that what you do shall affect what will happen (and so what you will perceive) while still stubbornly insisting in studying loops by cutting and pasting them as a concatenation of arcs. We often ignore the circular nature of behavior.

Part III

When stressing the importance of history for living organisms, a quick reply could be that geology is also concerned with it (geology was, of course, a source of inspiration for Darwin). Yet, nobody would claim that stones have personalities. There are indeed physical phenomena for which hysteresis is relevant, but memory is different in kind in living beings. Also (and this is again an important truism), living beings come into being, and so ontogeny is crucial. No doubt that is also key at the phylogenetic timescale. It is ironic that evolution is often presented as an example where theory generalizes (like in physics), when what evolution (arguably the most important principle in biology) precisely teaches us is that "living stuff" is inherently historical and radically contextual (which is precisely the opposite of the basic presupposition that works for "inert stuff": an electron is just an electron, regardless of when or where it is observed). There is no *ceteris paribus* in biology. Historicity gives rise to individuality, and so the object of biology is specific, not generic.

Conclusion

The current approach to behavior and its mechanisms could be characterized as "the Frankenstein error" (Figure 3), or the failure of the principle that what can be taken apart can be put together. There is no putting things that were pulled apart back together again. In our current automatized and sterilized approaches to behavior, we ignore the body, remove it from its natural context, and stop time. Integrative biology of behavior is needed more than ever. Our previous efforts to correct a reductionist bias may have left the impression that what animals and their brains do is of less importance than what they are made of (a move toward "functionalism") (Krakauer et al., 2017). What if, instead of chess—a classic example in functionalism—one plays another game instead: pool (billiards)? In this game, functioning is not irrespective of substrate but actually because of it. The "hardware" (the shape of the player, how long he or she has been playing, the length of the cue stick, the size of the table, and the quality of its felt) actually changes the nature of the question (and so its split with "software" becomes ill-posed). Substrate-irrelevant activities can be identically played any number of times, but there will never be two equal games of pool. Understanding behavior is not possible when it is taken out of context (Figure 3).

The behavior of animals is not the behavior of their brains. Behavior is not a broken loop. The behavior of the individual is not the behavior of the average. Living organisms are not just complicated systems (biologist zeitgeist) or just complex systems (physicist zeitgeist). We hope we have persuasively articulated the obvious so as to expose the nontrivial.

AUTHOR CONTRIBUTIONS

A.G.M. and A.A.G. conceived the project and wrote the manuscript.

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