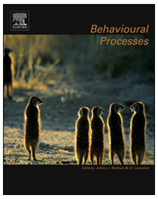
Behavioural Processes 167 (2019) 103892

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Timberlake's behavior systems: A paradigm shift toward an ecological approach

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ARTICLE INFO

Keywords:
Behavior systems
Ecological approach
Timberlake
Gibson

ABSTRACT

Timberlake's Behavior Systems model constitutes a discontinuity in theoretical and empirical consequences of traditional approaches to the experimental study of behavior, such as operant as well as classical conditioning. Here we consider the synergy of an animal-centered approach and acknowledge that niche-related behaviors as functional activities create synergy with Gibson's ecological approach, in at least three terms. These are: an ecological stance for learning and behavior, hierarchical organization of behavior systems, and affordances implied in the process of tuning experimental procedures. The ideas expressed herein favor a paradigm shift toward an ecological approach to behavioral science.

1. Introduction

When a new model is outlined in science, it is because certain phenomena and data need better explanations. The objective of this paper is to show that *Timberlake's Behavior System* (henceforth TBS) is a broad enough model to generate synergy for a paradigm-shift to the ecological approach championed by Eleanor Gibson (1969) and James J. Gibson (1966, 1979; Gibson, 1966, for a previous discussion see Cabrera et al., 2009a,b) and developed further by ecological psychologists (see Heft, 2001; Johnston and Turvey, 1980; Michaels and Carello, 1981; Reed, 1996; Stoffregen and Bardy, 2001; Turvey, 1992; Turvey et al., 1981). In order to forestall terminological confusion regarding the word 'ecological', adopting a strategy similar to that of Flynn and Stoffregen (1998/2011), we restricted the term 'ecological' when referring to Gibson's' ecological approach, and instead adopted the name 'Gibsonian approach'. In this paper, by the ecological approach we mean Timberlake's proposals when synergized with Gibson's.

The present paper discuses three parts of a rationale for arguing synergy with the Gibsonian approach: first, emphasis on portraying *ecological principles* of learning; second, behavioral units conceptualized as being subsumed into a *system* and third, environmental *tuning* seen as niche-centered procedures. All three reasons share the purpose of providing arguments for understanding aspects of behavior determined by the environment rather than by a mentalistic representational view.

Timberlake (1993a) acknowledges the concept of affordances (Gibson, 1979/1986) as useful for considering initial conditions in learning and part of the causal sequence of reinforcement. Nevertheless, we see a stronger linkage between the two. On the one hand, epistemologically the Gibson's approach is close to a behavioristic view that denies cognitivism: "James Gibson engaged in a sustained attack upon cognitivism over many years, from the thirties until his death in 1979" (Costall, 1984, p. 110, see also Morris, 2009). On the other hand, the Gibsons were convinced that learning does not happen fortuitously, by simply attaching a response to a stimulus or as an accrual of associations, but that animals are adapted to pick up meaningful information in their ecological niches, that a response is just a fragment of an adapted action (Reed, 1996), and that certain responses are favored depending on the species. "An animal learns what is functional and adaptive for its species" (Gibson, 1991, p. 97).

2. The Timberlake-Gibson ecological stance

2.1. A brief outline of the Gibsonian approach

Before building the 'Timberlake-and-Gibson' bridge, a brief description of the Gibsonian approach may be necessary, given its non-orthodox and innovative approach to psychology (Costall and Morris, 2015), and its wide influence upon diverse areas of knowledge, not only psychology, such as philosophy, arts, ergonomics, education, and design (see Covarrubias, Cabrera, & Jiménez, 2017; Covarrubias, Cabrera, Jiménez, & Costall, 2017. Interested readers will find a more detailed

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https://doi.org/10.1016/j.beproc.2019.103892
Received 13 February 2019; Received in revised form 16 June 2019; Accepted 21 June 2019

description in Heft, 2001; Michaels and Carello, 1981; Flynn and Stoffregen, 1998/2011). In brief, the Gibsonian view proposed that perception is not a cognitive act mediating distal and proximal stimulation, but is perception and information picked up directly from the environment. What an animal perceives from its environment is not based on sensory impressions enriched by cognitive or neural processes; the animal perceives ambient information directly from the invariants or non-changing properties in stimulation. That is, information occurs when an animal detects patterns in the environment's structured energy (light, sound, pressure, odor, etc.) that impinge on the perceiver. Most important for the purpose of this writing is that the Gibsonian approach connects perception with behavior, not just as independent systems but as an organism-environment system. Hence perception in organisms cannot be considered apart from behavior; perception necessarily involves behavior, it **is** behavior, and as such allows detection of more opportunities for action, named affordances.

The separation between perception and behavior is less an epistemological matter and more a case of artificiality in experimental procedures. Experimental procedures for perceptual studies (i.e., frozen images, darkrooms, tachistoscope-projected stimuli, etc.) impoverished information of stimuli and made it necessary to suppose that animals had to enrich and complete stimulation in order to complete perception, and then to behave. Gibson (1979/1986) saw the inadequacy of this reasoning and proposed that perceptual systems are whole body activities within the environment, so it is misleading to consider perception as prior to behavior, or see mental activity, like a 'ghost in the machine' as necessarily connecting the world with action through perception. Within these principles, the Gibsonian approach is naturalistic, compatible with a neo-realistic approach to studying behavior (Tonneau, 2011). We consider many of these arguments and their derivatives to be in synergy with those functional characteristics of TBS that we may embrace within an ecological approach.

2.2. An outline of the Timberlake view

Timberlake (1984) explicitly proposed the necessity of an ecological approach to understand and account for behavioral and learning processes. Historically, two contrasting perspectives on learning were identified. One emphasized controlled laboratory settings to research *general principles* of learning. Also known as an arbitrary *general-processes* approach, it favored the use of artificial problems, behaviors, and arbitrary stimuli. The other perspective is of *biological boundaries* as determinants of species' typical adaptations to specific environments (Blanchard, Brain, Blanchard, and Pargimiani, 1989; Johnston, 1981; Mason and Lott, 1976). Efforts to synthesize these two perspectives characterized Timberlake's approach. Timberlake argued that "learning should be studied in the context of natural problems, stimuli, and behavior" (Timberlake, 1984, p. 321), and that behavior even in restricted artificial laboratory settings is related to evolutionary determinants (Timberlake, 1990, 1993a,b, 2001a).

How ecological is the ecological approach? In the first instance, it is clear that the organism-environment interaction must be a main concern, but not mainly at the level of nutrient cycling, population regulation, or conservation. Timberlake's term 'ecological' refers to the "functional context in which learning evolved… considering the stimulus sensitivities, processing proclivities, response structures, and integrative states evolved to produce adaptive behavior in particular environments" (Timberlake, 1984, p. 324).

Based on its ecological stance, TBS allows communication among the wide-ranging views taken by behavioral ecologists and ethologists whose interests range from specific immediate outcomes of behavior in natural and semi-naturalistic contexts, phenomena studied by experimental psychologists that include motivation, learning, memory and perceptual processes, to evolutionary origins of behavior that can be mapped into fitness (Blanchard and Blanchard, 1988; Brain, 1989; Lorenz, 1978/1986). Thus, the ecological domain underlying TBS provides background for a naturalistic science of behavior and maintains the appropriateness of studying niche-related behavior of organisms in naturalistic and artificial environments (Timberlake, 1999, 2001a, 2002).

2.3. The Gibson-Timberlake synergy

Although the respective approaches are in many ways compatible, it is important to highlight differences. There is a marked difference between the meaning of 'ecological' in TBS and in Gibson's psychology. For Timberlake, an ecological background in psychology means anchoring psychological processes to niche-related mechanisms:

> "To the extent that behavior in laboratory learning paradigms has niche-related aspects, we would expect the responses, stimuli, and mechanisms involved to show typical evolutionary relations among species. In other words, there should be evidence of conservation of mechanisms within a particular phylogeny, and divergence as a function of ecological change." (Timberlake, 2002, p. 358).

Although this conviction coincides with Gibson's (1966; 1979/1986) view that ethological and psychological issues in animal behavior are circumscribed within an ecological and evolutionary framework (see Charles, 2017; Flynn and Stoffregen, 1998/2011; Reed, 1996), one main feature is deeply differentiated: the space and time scales for organism-environment system interaction. Whereas the appropriate temporal scale for ecology in the physical world ranges from substance absorption to long periods of genetic change and evolution, for Gibson the term 'ecological' is necessarily defined at the organisms' interaction level: "when physical sciences are considered in relation to organisms they become ecology, the study of the environment" (Gibson, 1966, p. 21). That is, for Gibson the term 'ecological' is used to describe the animal-environment system under relevant scales of space and time for the organism (Gibson, 1979/1986; Stoffregen, 2003). Events that are not relevant for the behaving organism are outside the scope of psychological science. That is the difference, Gibson argues, between the animal environment and the physical world. "We are concerned here with things at the *ecological level*, with the habitat of animals and men, because we all behave with respect to things we can look at and feel, or smell and taste (Gibson, 1979 p. 9). For instance, even if the erosion of a mountain is within the field of interest for ecology, given its extremely slow duration relative to the life of animals it is not in any way an *ecological event* for them. A rock falling from a mountain, however, while a minimal part of the erosion process, is at the ecological level for animals. For the organism-environment relationship, animal behavior must hence be studied at the ecological level (see Johnston and Turvey, 1980; Wagman and Miller, 2003).

Aside from the differences in use of the word 'ecological', even forgoing this term in the Gibsonian approach, both Gibson's and Timberlake's systems share an ecological stance rooted in evolutionary theory and nourished with ethological studies that seek general behavioral principles in natural, semi-naturalistic, and artificial situations, while considering principles of adaptation within the species' natural environments (Bitterman, 1975; Johnston, 1981; Krause and Domjan, 2017; Reed, 1996; Timberlake, 1999, 2001a,b). Therefore, artificial situations are used to "test hypotheses about learning as it occurs naturally, rather than serving as objects of study in themselves. The insights to be gained from the use of artificial conditions depend on the *contrast* with development under normal circumstances" (Johnston, 1981 p.135). Such circumstances include particular adaptive problems such as feeding, mating, orienting, etc., that are relevant to an ecological description of behavior. This rationale is further sustained by evidence that subjects tested in naturalistic environments show no advantages in performance over subjects in laboratory settings (see Gazes et al., 2012; Timberlake, 1990, 2001b); perhaps because "when an animal encounters an arbitrary (from the experimenter's view) task, it engages it with the nonarbitrary (evolved and developed) structure that most closely fits." (Timberlake, 1993a, p.122).

Furthermore, the ecological study of learning demands evolutionary thinking to identify selection pressures involved in learning (Johnston and Turvey, 1980; Reed, 1996) but the *adaptationist fallacy*, that is, speculative, unverifiable, and unfalsifiable explanations for adaptive behavior must also be avoided (Gould and Lewontin, 1979; Lewontin, 1979). These adaptationist arguments arise as reactions to biological boundaries when aiming to align with Darwinian adaptation principles. For a truly ecological approach it becomes necessary to differentiate between *ecologically relevant learning abilities* and *ecologically surplus abilities* (see Johnston, 1985). The former refer to particular animals' adaptations to their ecological niche over generations. Animals possess learning abilities that are revealed solely by the conditions under which they live. Other potential abilities will not be revealed because their natural environment does not support them. These relevant abilities are not the only ones, as artificial and experimental procedures support and reveal 'hidden', not naturally-prompted, abilities. Surplus learning abilities refer to those that do not contribute to actual adaptation to a niche, but are developed by animals within arbitrary environments, who cope with them according to pre-adapted underlying structure and genetic support (Johnston, 1982). These pre-adaptations correspond to TBS's perceptual-motor predispositions and initial conditions for learning (Timberlake, 2004) wherein experimental procedures must be appropriately designed (see Section 4).

3. The behavioral (perception/action) system

When an event is considered not by itself, but as a component of a system, a higher level of organization is assumed. Concerning such organization in the behavior of organisms, TBS relates the perceptual, motor, and motivational characteristics of organisms to an adaptive-evolutionary reasoning. A particular activity in animals must thus be understood as part of an adapted behavior system that "organizes and directs" such activity and its modifications (Timberlake, 1984).

Animals are "perceivers *of* the environment and behavers *in* the environment" (Gibson, 1979/1986, p. 8). Although behaving implies perception (Timberlake, 1994), and perceiving implies behaving (Gibson, 1966), both perception and behavior are constituted by different activities, nested within a system of perception and action (see Reed, 1996) in such a way that "we can now suppose that the *perceptual systems* develop perceptual skills, with some analogy to the way in which the *behavioral systems* develop performatory skills." (Gibson, 1966, p. 51, emphasis added).

On the one hand, considering the animal as *perceiver of the environment*, Gibson introduced the concept of a perceptual system as opposed to the classical concept of sensory channels (for a summary see Table 2). He argued the isolated and exclusive function of each sense untenable as a source of information; perception is not limited to a single sensory channel (Reed, 1985). Research has shown that visual centers, for instance, are not isolated in the brain but reside in various brain areas (an der Heiden and Roth, 1983a). Furthermore, Gibson (1966) asserts that

> "when the senses are considered as perceptual systems they are classified by *modes of activity* not by modes of conscious quality… some of the systems, moreover, will pick up the same information as others, redundant information, while some will not, and they will cooperate in varying combinations." (p. 49, emphasis added).

Hence, Gibson´s perceptual system conceives orienting, listening, touching, smelling, tasting, and looking as interrelated and cooperative acts for seeking out of information, not passive and mutually exclusive sensory channels.

On the other hand, considering the animal as *behaver in the environment*, Timberlake establishes a behavioral system opposed to the simple causal model in learning and behavior analysis (Table 1). Animal actions are neither arbitrary nor isolated, but are performed within an adaptive system in the niche animals themselves evolved (for an ecological view of action systems see Reed, 1982). Moreover, environmental objects and events are not completely simple nor arbitrary entities, but organizers and facilitators in the behavior system. TBS assumes that learning is not a process following a simple causal model (Timberlake, 1993a), but one occurring at different levels of a behavior system. That is, learning occurs through modifications in frequency, order and inclusion, as well as adjustments to mechanisms in the functional environment where the system evolved (Timberlake, 1983a, 1984). In addition, when an environmental element such as a reinforcer, "treated as an isolated causal entity loses contact with the context and becomes a meditational concept subject to the same vagaries that confront the use of more mentalistic concepts" (Timberlake, 1993a, p. 124), but treated as a biologically important element in the behavioral system, it "entrains a series of motivational search states expressed in organized sequences of related responses." (Silva and Timberlake, 2005, p. 99).

In TBS, each action is coordinated by four levels of a behavioral system. Briefly, the *system* level refers to a biologically important function in the organism, such as feeding, reproduction, parenting, defense, etc. The *subsystem* conglomerates "stimulus sensitivities, response components, and motivational states into strategies for advancing the function of the overall system" (Timberlake, 1994, p. 408). For example, predation is a subsystem of the feeding system in which mobile predators show a clear likelihood of chasing and capturing moving stimuli, or lying in wait at specific sites for ambushing predators.

Modes are "motivational substates underlying the sequential and temporal organization of appetitive strings of responses" (p. 408). This way, modes in a feeding system are defined according to the proximity to food; when food is remote general search occurs, when food is imminent focal search is observed, and finally, animals handle and eventually consume the food. *Modules* "represent groupings of stimulus filters, mechanisms of sensory integration, and motor components and programs" (p. 408). Timberlake talks of stimulus filters and sensory integration linking perception to motor components: "a moving object stimulates *perceptual filters sensitive to movement* that are related to responses such as chasing and capturing." (Timberlake, 1994, p. 408, emphasis added).

Research considering TBS has addressed different issues such as feeding (Timberlake, 1983a, 1994), social (Timberlake, 1983a; Timberlake and Grant, 1975), reproductive (Domjan, 1994; Domjan and Gutiérrez, 2019), defensive (Bouton, 2005; Fanselow, 1994; Perusini and Fanselow, 2015) and play systems (Pellis et al., 2019). However, other fundamental questions have to be addressed. What is the process by which an animal moves through the hierarchical system, from modes and modules to actions? How does transition from a general to a focal search arise? How does the animal enter handling and consuming mode? TBS highlights the predictability and proximity of the ecologically relevant element (prey in a feeding system, a female/male encounter in a reproductive system, and a threat in a defensive system). Silva and Timberlake (1998, 2005) found that explicit cues (e.g., lights) facilitated the distribution of search modes and responses in periodic schedules of reinforcement. Hence, modes potentially fall under the control of stimuli that are present during their expression. Thus, stimuli presented near food evoke responses related to focal search, whereas contextual cues (Domjan, 1994; Domjan and Gutiérrez, 2019; Silva and Timberlake, 1998) or stimuli presented distant from food evoke responses related to general search (Silva et al., 1998; Silva and Timberlake, 2005). In more general terms, information specific to the modes in the feeding process (i.e., search and general orientation, orientation to prey, and pursuit and capture of prey), connect the perceptual and action aspects of predation (see Reed, 1985).

Following the ecological principles outlined above (Section 2), not all stimuli are potentially successful at facilitating a given mode, but preorganized stimulus sensitivities and response patterns may resemble more natural eliciting cues (Timberlake, 1983a). For instance, given

Table 1
A comparison of traditional response model in learning and the behavior systems approach (See Timberlake, 1993a).

Traditional response model	Timberlake's Behavior System (TBS) model
The reinforcers as isolated and single events that strength the response	Reinforcer constraints the entire functioning system
Simple causal model	Multiple Causal system
Separate causal relation between response-to-consequence, and consequence-to-response	It is required linkage between consequence-response, and specifications of initial conditions and operating characteristics of the system
Initial responses preceding reinforcement are undifferentiated	Initial conditions preceding reinforcement are determinant for learned behavior
Centered in contingencies manipulated by the experimenter	Takes into account organismic and other situational variables
Learning occurs at the level of overt responding (as probability or rate of responding)	Learning occurs at the level of the system
Pavlovian and operant conditioning as different paradigms	Pavlovian and operant conditioning constrain the same underlying system.
Reinforcer as constructor of behavior	Reinforcer as modifier of an already-functioning system
The scope of variables related to: rate, frequency, temporal/spatial variables	The scope of variables related to: stimulus support, disequilibrium conditions, memory, stimulus processing and integration, selection environment.

that rats are social feeders, their predatory behaviors are incorporated into a social pattern when another conspecific is presented as a predictor of food (Timberlake and Grant, 1975), but not hamsters, which are solitary feeders, and hence their predatory behaviors are separate from the social system (Timberlake, 1983a). Other consistent evidence shows that when the spatial distance of levers for rats (Silva et al., 1998), and direction of visual stimuli for pigeons (Cabrera et al., 2009a,b) are near/toward the food-site, subjects engage in more responding than when the distance/direction is away from it. Also, behaviors directed to a rolling ball were higher and more vigorous when the food system (food deprivation) was made more salient than the water system (water deprivation) (Timberlake, 1983b).

In the TBS research program, empirical output has mainly depicted the behavior systems' first three levels (system, sub-system, and mode); particularly transition from general to focal search, and then to handling and consumption. The behaviors (actions) related to such modes are identified as locomotion, paw grooming, rearing, time spent standing at greater or lesser distance from the feeder, lever pressing, nosing the feeder, etc. Nevertheless, detailed description at the module level has often been neglected; that is, this level has been described by perceptual-motor modules, "groupings of *stimulus filters*, mechanisms of *sensory integration*, and *motor components*" (Timberlake, 1994, p. 408, emphasis added). Thus, modules "can be viewed as candidates for different sequences of behavior … The sequence that occurs in a particular circumstance will be determined by the way in which these possible links interact with the environmental stimuli and constraints." (p. 410).

The module level is not entirely depicted by the behavior itself, but entails environmental support for that behavior. Timberlake (1983a, 1999) argues that perceptual-motor modules determine the sequence of responses elicited and controlled by particular stimuli (i.e., environmental supports) in a probabilistic way that, if appropriately tuned, facilitate or constrain animal action patterns.

What are the perceptual-motor modules that prepare the subject to respond to particular stimuli with particular actions? The animal perceives objective opportunities and restrictions according to its capabilities and skills. Is that surface walkable? Is it climbable? Is that object reachable and graspable? Is that prey bitable, edible, and chewable? That is, environmental information about opportunities for action, or affordances, becomes necessary for the TBS model. Given that this perceptual-motor organization of behavior systems resides at the module level, a theory of perception and action is needed.

4. Environmental tuning and the theory of affordances

> "An ecologically based approach assumes that the behavior of a hungry rat in an experimental chamber is evolutionarily based on evolved mechanisms that can facilitate locating and consuming food, even in an artificial environment, *if it is appropriately tuned*." K.M. Silva and Timberlake, 1998, p. 192, emphasis added).

Timberlake (1999, 2004) refers to *tuning* as the process of developing procedures, designing and building an apparatus to foster emergence of interpretable behavior in a laboratory setting. Tuning is thus creation of an environment adjusted to the animals' functional-perceptual-motor framework in order to support behavior of interest.

The process of tuning the apparatus and experimental procedures is highlighted within the TBS framework; it is so important that we may definitely assert that apparatuses are full of theory. In other words, well-tuned apparatus construction is a theoretical activity.

Timberlake argues on several occasions (Timberlake, 1983a, 1994, 2001a,b, 2002, 2004; Timberlake and Lucas, 1989) for tuning and configuration of objects, surfaces, and events into experimental apparatuses, as the species under observation (Timberlake and Hoffman, 2002; Timberlake and Washburne, 1989) determines many of the response strategies (Hoffman et al., 1999; Roche and Timberlake, 1998; Timberlake, 1983c; Timberlake et al., 1999).

Timberlake (2001b, 2004) notes that Skinner was keenly aware of the attunement of the apparatus and procedures;

> "how he successively modified his operant chamber and lever to promote lever pressing, including lowering the ceiling, moving the lever higher on the wall and closer to the feeder, and eventually, rounding the end of a lever that barely protruded from the wall" (Timberlake, 2001b, p. 165).

Timberlake continues along the same route and relates the

Table 2
A comparison of traditional perception approach and the perceptual systems approach (see Gibson, 1967).

Traditional sensory model	Gibson's Perceptual System approach
Bundles of nerve fibers connecting receptors with specific points in the brain	Incoming fibers and outgoing fibers
Passive receptors	Active orienting and exploratory adjustments
Mutually exclusive	Overlaps one another
Yield awareness of receptors stimulated by amounts of energy, radiant, mechanical, thermal, or chemical.	Yield awareness of objects and events
Perception as the outcome of stimulation derived from sensory receptors: retina, cochlea, skin, tongue, nasal membrane.	Perception as acts: looking, listening, touching, tasting, and sniffing.
Reaction to stimulation	Pickup of ambient information
No subject to modification by learning	Amenable to modification by learning

behavioral effects when beginning to manufacture custom devices, such as rolling balls that signaled food (Timberlake et al., 1982), and levers which

> "By slightly changing the lever's dimensions and location, we could (inadvertently) support nosing underneath, biting, grasping, shaking, or two- and one-handed presses. Together, these results support the existence of an underlying repertoire of perceptual-motor units that can emerge and change, tracking changes in the stimulus conditions despite a long history of reinforcement." (Timberlake, 2001b, p. 165).

Those behaviors that appear when tuning the levers and rolling balls are not matters of chance, but the *underlying repertoire of perceptual-motor units* that emerges from specific interaction between the animal's initial conditions and its niche. In artificial laboratory settings a good match between the subject's conditions and the apparatus guarantees reliable results; if objects, surfaces, and events of the apparatus are appropriately tuned, action patterns match niche-related mechanisms of evolved behavior in that animal; but if mistuned the objects, surfaces, and events provoke maladaptive behavior. When mismatching occurs, misbehavior emerges. A parallel occurs in laboratory studies of perception: when artificially reduced information is presented, misperception and illusions are reported (see Gibson, 1966)[1] .

For TBS the procedure and apparatus thus become as important as the animal's body and sensory capabilities (Burghardt and Bowers, 2017). For this mutuality of environmental circumstances and the organism's properties, Gibson (1966, 1979/1986) coined the term *affordance*, meaning "what the environment offers the animal, what it *provides* or *furnishes*" (Gibson, 1979/1986, p. 127). In short, environmental events and surfaces provide opportunities for action to a given organism (see Jones, 2003), in which the "the composition and layout of surfaces constitute what they afford" (Gibson, 1979/1986, p. 127).

Recently, the relevance of affordances in the attunement of operant procedures has been described experimentally. For instance, Cabrera, Sanabria, Jiménez, and Covarrubias (2013) showed that the lever protruding from the wall constitutes an affordance for lever pressing in rats and hamsters exploring the operant chamber, and the latency and frequency of such lever pressing changed as a function of the lever height relative to subjects' body size. This result was replicated when lever pressing was reinforced according to single and concurrent schedules of reinforcement (Jiménez et al., 2019, 2017), as well as in a test of reaching behavior (Cabrera and Ortega, 2017) where food had to be reached and grasped through an orifice: frequency and limb preference changed as a function of the orifice's diameter and height. In all these experiments, tuning some important elements in the apparatus (i.e. the lever or the orifice) according to subject size produced more responses. The value of affordances has also been observed in the object exploration task (Heyser and Chemero, 2012), where the exploration pattern in mice is seen as a function of what the object structure furnishes for the animal; if the object is climbable, then subjects explored longer and were more resistant to habituation than when the object was only touchable (see Chemero and Heyser, 2005).

Hence, the process of tuning is the process of building appropriate affordances for the animal in experimental situations. The TBS approach "acknowledges the affordance of the specific, current environment and the effectivities of the body" (Burghardt and Bowers, 2017, p. 357) and "knows what to do with evolution and is clear about how the affordances of the environment and effectivities of the body are essentially tied to the evolution of motivational systems." (p. 352).

Indeed affordances, while initially described as facts of environment as well as behavior (Gibson, 1979/1986), are often analyzed by highlighting either facts of the environment or the effectivities, or abilities, of organisms. That is, the *affordance* is referred to as a dispositional property of the environment whose complementing disposition is the *effectivity* of the animal (see Scarantino, 2003; Turvey, 1992). Effectivity, as a propensity of the animal to effect some movements given its body structure, phylogenetic and ontogenetic processes, when overlapping or juxtaposed with certain environmental features becomes the behavioral emphasis of the affordance. Further, when the structure, design, and other ecological properties of the surroundings match an animal's effectivities, those environmental surfaces, objects and events become the environmental emphasis of the affordances. Roughly speaking, the "affordances tell us what to do, and effectivities tell us how to do it" (Shaw et al., 2017, p. 28). For example, in a procedure where rats have to use their forepaws to reach food through an orifice (Cabrera and Ortega, 2017), the affordance is enacted by the food located in the orifice of such and such diameter and height, and effectivity indicates behavioral topography (i.e., posture and right or left forelimb) to reach the food.

Affordances, then, make it more probable that animals will attend to and engage in certain behaviors rather than others within the environment's multiple concurrent (Mangalam and Fragaszy, 2015) and nested (Wagman et al., 2016) affordances. However, for the affordance to be effective, the animal must fulfill two conditions: A motivational state that activates the animal for a goal-directed action, and the perception of environmental resources to achieve that goal (see Greeno, 1994; Reed, 1985). In this context, for a food-motivated organism, food is a resource for ingestion, and objects, places, and events are perceived as potential resources for finding prey. Hence, animals will show a tendency to seek places from which prey can be observed, pursued, and eventually eaten (Reed, 1985, p. 373). The motivation to engage in some actions over others will depend partially on the resources required. The feeding system guides attention to signals for food more accurately than signals for reproduction, but not if a mating system is currently active. The animal will be more attentive to those features of the environment offering more consistent opportunities for reaching the biological element that defines the actual motivating system (i.e., feeding, mating, nesting, etc.).

In terms of affordances theory, attunement in the TBS approach is not only that which the experimenter builds and designs into experimental procedures to furnish and facilitate specific action patterns for the animal. Rather, attunement from the animal's side involves sensitivities and abilities to the built environment, whether appropriately tuned or not. That is, TBS assumes that, because the animal's adapted endowments "necessarily fall back on the same stimulus processing and response repertoire engaged in more natural settings" (Timberlake, 2001b, p. 161), *misbehavior* findings are comprehensible and expected (Breland and Breland, 1961) as alternative responses the experimental setting affords to the animal (Timberlake, 1999; Timberlake et al., 1982).

In summary, if a niche is a set of affordances (Gibson, 1979/1986), and the experimental procedures seek to create ties to natural niche-related behaviors compatible with appetite, defense, reproduction, parenting, etc. (Timberlake, 1999), then attunement is twofold, with the researcher's action in designing behaviorally relevant surfaces and procedures, and the organisms' perceptual and motor abilities for coping with them. Animals have adapted to specific niches and learn from environmental constraints in such a way that

> "the perceptual abilities of organisms change on both evolutionary and developmental timescales. Once perception is understood as an adaptation to the existence of structured energy, we can understand evolutionary and developmental processes as 'tuning' the perceptual systems of organisms. That includes tuning the behavioral systems that are dynamically entwined with perception… The conceptual shift toward seeing the world as composed of behaviorally relevant

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[1] A similar effect has been discovered with the human environmental mismatch. Since human advancements have deeply modified the naturally-evolved human niche, the evolutionary mismatch has produced health and social problems (Blaisdell, 2017).

> elements leads to the concept of 'affordances.'" (Charles, 2017, pp. 207-208).

The behaviorally relevant elements in the world for a species are then the fundamentals for tuning, since

> "The key to tuning is to focus on the apparatus configurations and procedures that support and promote niche-related proto-elements that are compatible with the motivational state, perceptual-motor organization, environmental support, and schedule… Modifying apparatuses and procedures and shaping behavior represent a two-way interaction between the experimenter and the subject, a sort of negotiation between the experimenter's support and criteria and the organism's repertoire of mechanisms." (Timberlake, 2004, pp. 212-213).

5. TBS as a nested system

The TBS emphasis upon function and niche-related mechanisms relevant to specific activities and animals is not a conjectural nor *ad hoc* explanation, but specific and tied to real possibilities the animal encounters in its surroundings, with action patterns nested in larger units that function as corresponding nested affordances to describe the hierarchical system of behavior.

In an early description of TBS, Timberlake (1983a) depicts a behavior system as "a set of modules loosely organized in semi-hierarchical fashion such that some modules normally precede or follow other modules" (p. 184). This description is straightforward for a behavior organization entailing a probabilistic sequence within its units:

> "In the behaviour system model, each system is composed of smaller organized units of perceptual-motor organization which I will call modules. Each perceptual-motor module consists of responses that show a probabilistic sequential and/or temporal relation, and are probabilistically elicited, controlled, and terminated by particular stimuli. These modules may vary considerably in their degree of initial integration and the fineness of their perceptual-motor tuning." (p.184).

Later (Timberlake, 1990, 1994, 1999), TBS distinguished modes from modules. The former denotes stimulus sensitivities and motor repertoire based upon *sequential aspects* of behavior, from general search to a consummatory act, to fulfill the particular function (i.e., eating). The latter denotes *attentiveness* to specific stimuli, and tendencies to respond with specific motor components.

Attempting to understand the specific function of perceptual-motor modules in TBS, the theory of affordances becomes a framework from which action patterns observed in animals (lower level in Fig. 1) are hierarchically organized as multiple nested affordances (Wagman et al., 2016), or otherwise expressed in nested activities (see Baum, 2002, 2004). That is, to accomplish a superordinate action in the hierarchy, a sequence of activities furnished by objects and events in the environment is required; emerging at each level of the hierarchical organization and eventually reaching the higher level category. The motivational system is defined according to the required resource type (i.e., food, mate, territory, etc.), while the subsystem is characterized by sensitivities, motor components and strategies of the predator. For example, different sensitivities and response components emerge if it is a mobile or a lie-in-wait predator. Modes are defined according to the time/distance horizon and imminence of encountering said resource (general search, focal search, and handling or consuming). Modules are specific action patterns, depending on opportunities for action the animal perceives through its phylogenetic and ontogenetic endowments, nested within a particular motivational system.

Though other behavior systems developed in the ethological domain were relevant for the advancement of TBS (for an overview see Bowers, this issue; Bowers, 2018; Burghardt and Bowers, 2017), a TBS hallmark that becomes suitable for describing nested affordances is related to its functional nature.

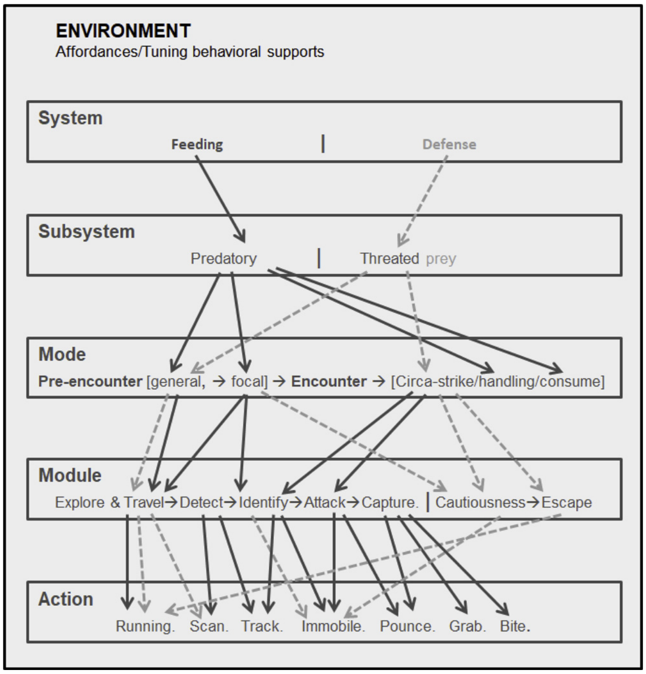

Fig. 1. A scheme of the nested behavior system. Levels of the nest from top to bottom. In the mode and module boxes the horizontal arrows indicate range from most general to most specific level. See main text for a detailed description.

Fig. 1 shows a version of TBS as a nested system, comparing the feeding and defense systems (arrows from upper to lower levels indicate the sequence from superordinate to subordinate levels in the hierarchy). The first and second boxes define the system and subsystem that correspond to the motives and goals by which the animal performs an action. The continuous black arrows define a feeding system, and the dashed grey arrows represent a defense system. The mode level is what the animals perform according to spatiotemporal imminence of the prey or predator. This corresponds to what the animal does in a feeding or defense context, but time and distance from the goal also become relevant. Modules and action patterns correspond to the means by which specific actions respond to stimuli and events.

Fig. 1 shows the whole system surrounded by the environment, whether in natural or experimental settings, with affordances and tuning representing the environmental niche for objects, surfaces, and events that are behaviorally relevant to the organism at all levels. For instance, the feeding system could be identified as time since the last meal (see Collier, Hirsch, and Hamlin, 1977), whether naturally or procedurally attuned, and possibilities for seeking prey. Defense is tuned by detecting a threatening situation or attuning aversive stimuli with options to hide, escape, or fight[2] . However, the behaviors under observation are the specific activities and topographies for such an action pattern (lower box in Fig. 1), and movements employed with objects in the world (Domenici and Black, 2000) and task-specific devices (see Bingham, 1988). Henceforth, one specific behavior could be nested in different systems: for instance *running* (lower box) could be observed in a forager within a feeding system (black arrows) or in escaping prey (gray dashed arrows) within a defense system. In the same way, *immobility* could be observed in the predator (while lying in wait),

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[2] Note that a defense system is active only after the threatening situation. Before that, when the predatory imminence is low, the animal behaves under some other system such as feeding, mating, etc. (See Fanselow and Lester, 1988).

or in the threatening prey (freeze reaction). While the same behaviors are observed, they are nevertheless nested in different hierarchical systems.

6. Conclusion

Paraphrasing Killeen (2018), the study of animal behavior "has a data glut and a theory insufficiency" (p. 124). Perhaps the theoretical endeavor to explain behavior requires a paradigm shift. For the above-noted reasons, and arguments expressed at the 'Special Symposium of Behavior Systems and the legacy of William Timberlake' as part of the XIX Biennial Meeting of the ISCP (2018), Timberlake's whole scientific output, not just the TBS research program, incites a paradigm shift toward an ecological approach. Coinciding with some other proposals (Baum, 1995, 2012; Killeen, 1984; 2018; Rachlin, 1992), Timberlake manifests the necessity of a more comprehensive view of experimental behavioral analysis:

"It seems shortsighted to ignore potentially relevant information available from a consideration of proper function, niche-related mechanisms, and evidence from other approaches. Such a strategy tends to isolate operant concepts from further development and unnecessarily limits forging profitable ties with other approaches." (Timberlake, 2004, pp. 203).

In the same manner, coinciding with some ethologists (Blanchard et al., 1989; Brain, 1989; Burghardt, 1973), Gibsonian psychologists (Johnston, 1981, 1985; Johnston and Turvey, 1980; Miller, 1985; Reed, 1985, 1996) and comparative psychologists (Mason and Lott, 1976; Shettleworth, 1989), Timberlake calls for an attitude reconciling experimental psychology and ethology, to integrate their research programs:

> "Because both ethological and laboratory learning approaches have produced reliable and influential analyses of behavior, I believe it is important to try to integrate the two in a common conceptual framework… A significant problem in this endeavor, though, is to convince proponents of each view that integration is worthwhile and possible." (Timberlake, 2002, p. 355).

In conclusion, our proposal in this tribute to Bill Timberlake is that TBS strategically moves experimental psychology from an entrenched position into field-oriented ethology, accomplishing an ecological revolution in behavioral science, with Bill Timberlake as a valiant commander in said scientific revolution, challenging constraints to learning in terms of ecologically defined behavior systems. The Gibsonian represents an allied approach to the TBS endeavor, given their distinct theoretical alternatives to mainstream theories (Reed, 1985), but relying upon sufficient epistemic principles for harmony with a behavioristic approach (Costall, 1984; Covarrubias, Cabrera, & Jiménez, 2017; Covarrubias, Cabrera, Jiménez, & Costall, 2017; Guerin, 1990; Morris, 2009; Tonneau, 2011), and the fundamentals for transforming experimental psychology, particularly behavior analysis. Thus, TBS affords a paradigmatic shift for the study of behavior, into an ecological approach, with a broader view to overcoming the vexing conflicts that arise between models in a science of animal behavior.

Acknowledgements

The authors thank Aaron Blaisdell, Robert Bowers, Andrew Wilson, and two anonymous reviewers for helpful comments.

This work was supported by Consejo Nacional de Ciencia y Tecnología, CB-2012/180443(Felipe Cabrera).

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