Beyond single discrete responses: An integrative and multidimensional analysis of behavioral dynamics assisted by Machine Learning

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Abstract

Behavioral systems, understanding it as an emergent system comprising the environment and organism subsystems, includes the spatial dynamics as a basic dimension in natural settings. Nevertheless, under the standard approaches in the experimental analysis of behavior that are based on the single response paradigm and the temporal distribution of these discrete responses, the continuous analysis of spatial behavioral-dynamics has been a scarcely studied field. The technological advancements in computer vision have opened new methodological perspectives for the continuous sensing of spatial behavior. Derived from them, recent studies suggest that there are multiple features embedded in the spatial dynamics of behavior, such as entropy, and that they are affected by programmed stimuli (e.g., schedules of reinforcement), at least, as much as features related to discrete responses. Despite the progress, the characterization of behavioral systems is still segmented, and integrated data analysis and representations between discrete responses and continuous spatial behavior, are exiguous. Machine Learning advancements, such as t-SNE, variable ranking, among others, provide invaluable tools to crystallize an integrated approach for the analysis and representation of multidimensional behavioral-data. Under this rational, the present work: 1) proposes a multidisciplinary approach for the integrative and multilevel analysis of behavioral systems; 2) shows behavioral aspects usually ignored under the standard approaches in the experimental analysis of behavior; and 3) provides sensitive behavioral measures, based on spatial dynamics, and useful data representations for the study of behavioral systems. In order to exemplify and evaluate our approach, the spatial-dynamics of behavior embedded in phenomena relevant to the behavioral science, namely *water-seeking behavior* and *motivational opera*tions, is examined, showing aspects of behavioral systems hidden until now.

Keywords: Behavioral systems; spatial-behavioral dynamics; time-based schedules; water-seeking behavior; motivational operations; Machine Learning; t-SNE; entropy

The main objective of the Behavioural Science is to account for the principles that underlie in the Behavioural System, understanding it as an emergent and complex system comprising an environment and organism subsystems (Gibson, 1979; Kantor; 1970; Kuo, 1976; Timberlake, 1994; Turvey, 2018). In the Behavioural System, the bioecological relevance of the events and segments of the environment are codetermined by the qualities of the organisms and its response systems, defined in a phylogenetic and ontogenetic way. In simple words, the principal goal of the Behavioural Science is to describe the principles and processes of the *natural* behaviour. As has long been established, *natural behaviour* includes Spatio-temporal dynamics as a basic dimension, one of the obvious and elemental expression of these dynamics are the approach-withdrawal patterns (Schneirla, 1959), and its direction and vigor (Duffy, 1951, 1957).

Nevertheless, for various reasons, in the history of the experimental behavioural science, discrete-response analysis gained prominence over the analysis of locomotion patterns and its dynamics. One reason for this was the affordable technology available at the end of the first half of the last century to make reliable and automatized records of behavior. These records were made primarily through the use of mechanical and electronic switches (Escobar, 2014). The analysis of the records focused on the computation of the frequency and temporal distribution of the activation or deactivation of switches (e.g., total number of responses to an operand, number of responses per unit of time, inter-response times, etc.). The predominance of apparatus, measures, data analysis and data representations based on discrete events or responses (e.g., lever press, nose poking, water or food dispenser entrance) had as a consequence that the Spatio-temporal dimension of behaviour has been generally ignored or, in the case it was considered, it was discretized or reduced to first order measures (e.g., time spent in a given zone of the experimental arena). From this, it follows that standard approaches in the experimental behavioral science do not account for the dynamics that emerge from the movement of the organism and its behavioural continuum (León et al, 2020b).

Fortunately, with the computational advancements made in the last decade in computer vision, machine learning and, specially, deep learning techniques, the use of tracking systems has become more popular (Dell, et al., 2014; Mathis & Mathis, 2020; Pérez-Escudero, et al., 2014) for the recording and measurement of the Spatio-temporal

behavioural continuum. These relevant technological advances in the recording of behaviour have opened new methodological and theoretical perspectives in the behavioural science. One of these perspectives is the integrative approach between discrete environmental events and discrete responses with relevant variations of the environment and the Spatio-temporal dynamics of behaviour subjacent in a wide variety of behavioural phenomena and species (Loveless & Webb, 2021; León et al., 2020a; León et al., 2020b; Maekawa, et al., 2020).

Natural behaviour includes complex interactions between different behavioural patterns and multiple aspects of the environment that are difficult to apprehend with the methodological standard approaches of the single-response record in the Experimental Analysis of Behaviour. And while this issue was pointed long time ago and was tried to solve (see Henton & Iversen, 1978), the application of computational methods, both in sensing instruments and in the analysis and representation of multidimensional data based on machine learning, currently provide invaluable tools (Datta, 2019; Mathis, et al., 2018; Marshall et al., 2020; Torabi, et al., 2020) that allow to crystallize an integrated approach for the analysis and representations of complex behavioural-patterns and Spatio-temporal dynamics of behavior. This approach could show aspects of the behavioural phenomena, hidden until now to the behavioural science and, more specifically, to experimental psychology. This emergent multidisciplinary approach could be named computational-experimental psychology or computational-experimental analysis of behavior.

Under this novel approach, in the present work we present two examples, using a subset of datasets from our laboratory (León, et al., 2020a; Hernandez, et al., 2021), of an integrative analysis and data representation using machine learning tools, in order to account for the spatial-dynamics of behaviour embedded in phenomena relevant in the behavioural science, namely water-seeking behaviour and motivational operations. Our work integrates recording for continuous spatial behavior (based on machine vision), discrete responses of the organisms with multiple measures for each one (first-order -such as *velocity*, *distance to focal points*, etc.- and non-first order - *entropy* and *divergence*-), multilevel data analysis (within-subject, within-session; between subjects, between sessions), and finally, multidimensional representations, based on machine learning, for the unitary system between Spatio-temporal dynamics and discrete responses (see Figure 1).

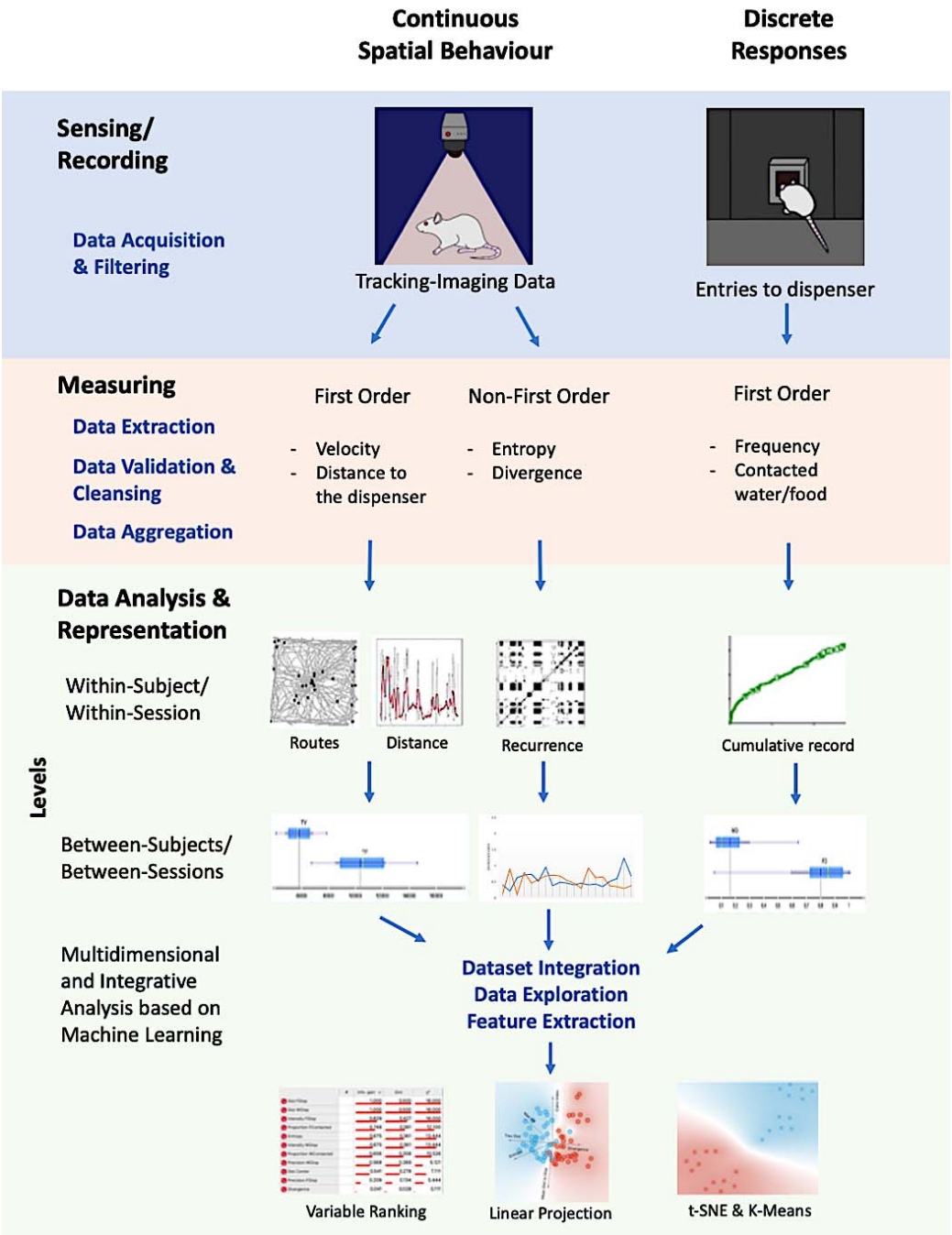

Figure 1. Graphical representation of the proposed integrative, multilevel and multidimensional approach. It integrates recordings for continuous spatial behavior (based on machine vision), discrete responses of the organisms with multiple measures for each one, multilevel data analysis (within-subject, within-session, between subjects, between sessions), and a multidimensional characterization of the unitary system between Spatio-temporal dynamics and discrete responses.

The purposes of the present work are: 1) to propose a multidisciplinary approach for the integrative and multilevel analysis of behavioral systems; 2) to show some behavioural aspects, revealed under the proposed multidisciplinary approach, usually hidden under the standard approaches in the experimental analysis of behaviour; and 3) to provide some sensitive behavioural measures, based on spatial dynamics, and useful data representations for the study of behavioural systems.

Example 1

Water-seeking behavior: Behavioral dynamics under fixed and variable temporal schedules

One of the most significant contributions of the Experimental Analysis of Behaviour for the comprehension of the variables that underlie behavioural phenomena are stimuli schedules (e.g., schedules of reinforcement; Ferster & Skinner, 1957). A stimuli schedule is a rule, defined in a systematic and parametric way, for the presentation of stimuli (e.g., water, food; Reynolds, 1975). The stimuli schedules can be categorized according to several criteria, one of the most common and useful is contingent vs. non-contingent schedules. The first one, in methodological terms, is usually associated with 'operant-contingencies' and the second one with 'pavlovian-contingencies'. The difference between contingent and non-contingent schedules is that in the first one, the occurrence of a given stimuli is dependent (or contingent) to a given response of the organism (e.g., lever presses), whereas in non-contingent schedules the presentation of the stimuli does not depend on any organism's response but only on the temporal relation between the stimuli. In *strictu sensu*, these last are named time-based schedules.

There is a wide corpus of research, with both kind of schedules, with several species and apparatus (Boren et al., 1978; Lachter et al., 1971; León, et al., 2020a; Hernandez, et al., 2021; Zuriff, 1970). Most of this research is based on the recording and data analysis of a discrete single response, especially with 'appetitive' stimulation. The basic data are head-entries to a food or water dispenser and food pellets or drops of water consumed, in other words, the temporal distribution of a given discrete response. In a few studies, the data was extended to time spent in zones near to a dispenser (Baum, W. M., & Rachlin, 1969). With time-based schedules, different behavioral phenomena have been studied, for example,

‘superstitious behavior’ (Reberg et al., 1977; Skinner, 1948), ‘timing’ (Drew et al., 2005; Sanabria et al., 2009), among others. From a systemic and parametric approach, these different phenomena could be characterized as behavioural systems and their corresponding spatial-temporal dynamics. The two time-based schedules, fixed and variable, have been scarcely studied, in a comparative way, this contrast with studies that have compared fixed and variable contingent schedules (interval and ratio schedules). On the other hand, there are not comparative-studies that explicitly included the spatial dimension of behaviour and its dynamics, under these fixed and variable temporal schedules, neither that integrate the standard data, based in discrete responses, with continuous data based in locomotion. Under this rationale, we evaluated the spatial dynamics of behavior in Wistar rats under two temporally water delivery-schedules (fixed and variable-time schedules) in a Modified Open Field System (MOFS), from an integrative analysis and data representation perspective, using machine learning tools.

Method

Subjects

Four experimentally-naïve, female Wistar rats were used, two rats were assigned to a Fixed-Schedule Condition and two rats to a Variable-Schedule Condition. All rats were three-months old at the beginning of the experiment. Rats were housed individually with a 12-hr light and dark cycle and maintained under a daily schedule of 23 hours of water deprivation with free access to water 1 hr. after experimental sessions. Food was freely available in their home cages. One session was conducted daily, 7 days a week. All procedures were conducted in agreement with university regulations of animal use and care and followed the official Mexican norm NOM-062-ZOO-1999 for Technical Specification for Production, Use and Care of Laboratory Animals.

Apparatus

A Modified Open Field System (Model WEOF by Walden Modular Equipment) was used. A diagram of the apparatus can be found in León, et al (2020a). Dimensions of the chamber were 100 cm x 100 cm. All four walls of the chamber as well as the floor were made of black Plexiglas panels. A water dispenser (by Walden Modular Equipment), based in a servo system, when activated delivered 0.1 cc of water on a water-cup that protruded from the center of the MOFS. The MOFS was illuminated by two low-intensity lights (3

watts) located above the chamber and in opposite sides of the room in order to avoid shadowed zones. Once delivered, water remained available for 3 s. A texturized black patch, 9x9 cm with 16 dots/cm, printed in a 3d printer was located in close proximity to the water dispenser in order to facilitate its location.

The experimental chamber was located on an isolated room on top of a table of 45 cm of height. The room served to isolate external noise. All programmed events were scheduled and recorded using Walden Tracking System (v.0.1). Rats' movement was recorded by a Logitech C920 web camera, located at the center, 1.80 mts. above the experimental chamber. Tracking data was analyzed using Walden Tracking System (v.0.1). This software recorded rats' location every 0.2 s in the experimental space using a system of X, Y coordinates. The system recorded the rats' location according to their center of mass. Data files obtained from this software were then analyzed using MOTUS® and Orange 3.26 Software.

Procedure

Subjects were exposed to one of both conditions of water delivery: a) Fixed Time (FT) 30 s schedule or b) Variable Time (VT) 30s schedule. Each condition lasted 20 sessions. Each session lasted 20 minutes. Rats were directly exposed to the conditions without any previous training. Two rats were assigned to Condition 1 (FT) and two rats to Condition 2 (VT).

Results

In order to characterize the behavioural continuum and to compare the spatial-dynamics of behaviour under fixed and variable time schedules, we conducted an integrative and multilevel analysis. First, we present representative within-subject results of the behavioural continuum within sessions, for the first, intermediate and last session of the experiment, for one representative subject for each condition. Second, we show summary results for measures based on spatial behaviour, of first and non-first order (entropy and divergence), and a measure based on discrete responses (coincidence index). Third, we present a multidimensional analysis and integrative representation based on Machine Learning.

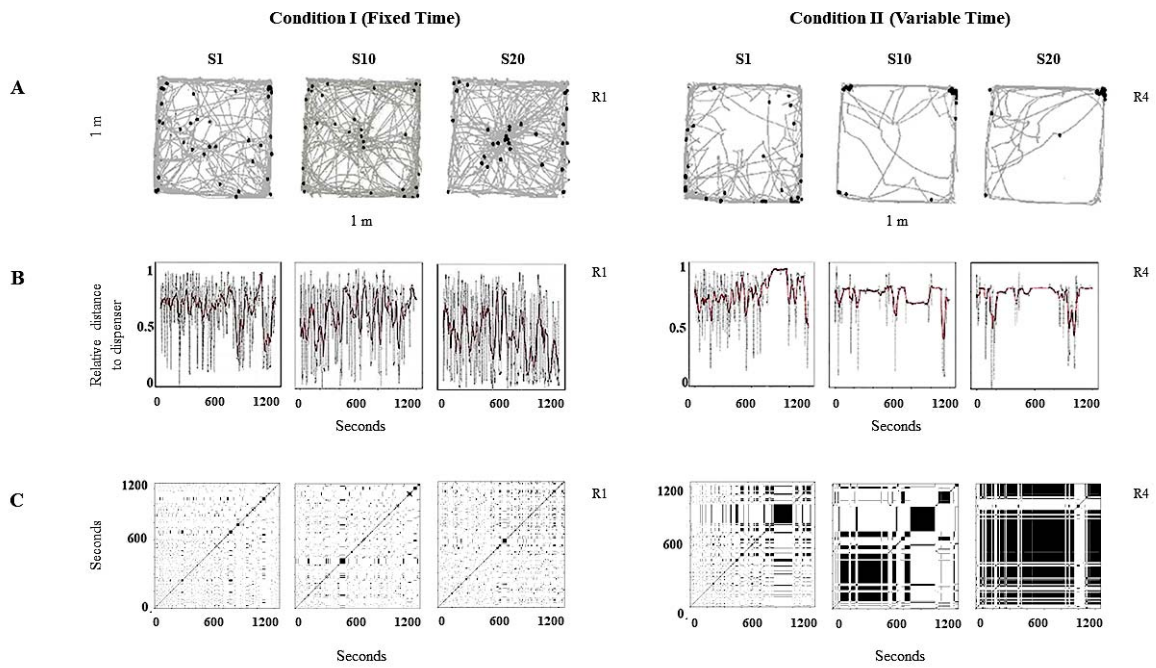

Figure 2. Representative within-subject results of the behavioral continuum for the initial (Session 1), intermediate (Session 10) and last session (Session 20) for one rat under Fixed Time (R1, left panels) and one rat under Variable Time (R4, right panels). Each column depicts a session. Panel A shows the routes of the rat (grey lines) and rat's location at the moment of water delivery (black dots) in bidimensional representation of the experimental chamber; Panel B depicts the relative distance to the dispenser (Y axis) moment-to-moment (X axis); and Panel C shows recurrence plots. See text for a complete description.

Figure 2 shows routes (Panel A), relative distance to the dispenser (Panel B) and recurrence plots (Panel C) for one rat under Fixed Time Schedule (Rat 1, left section) and one rat under Variable Time Schedule (Rat 4, right section). Each column corresponds to a given session (1, 10 and 20). In Panel A, in a bi-dimensional representation of the MOFS, the routes of the rat (grey lines) for the whole session, and rat's location at the moment of water delivery (Location at Water Delivery, LWD) are presented (black dots). Three findings are worth mentioning: 1) routes were more extended under Fixed Time (FT) than with Variable Time (VT); 2) for both conditions, a progressive change in the direction of the routes was observed, toward the water-delivery zone, as the sessions progressed; and 3) the LWD gradually got closer to the water dispenser as the experimental sessions progressed. Panel B shows the relative value of the distance from the rat to the dispenser

every 0.2 s (grey dots). In addition, in order to show the tendency of the distance function, we performed a smoothing of it (red line) by using a moving average of 200 frames (i.e., 40 seconds, see equation in the supplementary material). With this measure, a value close to 1 indicates that the distance from the rat to the dispenser was the maximum possible and value close to zero indicates that the rat was located in close location in relation to the dispenser in a given time (frame). In both conditions, a back-and-forth pattern was observed (grey dots), but this was clearly more pronounced and had shorter periods under FT than in VT. On the other hand, the moving average (red line) suggests a tendency, under both conditions, to reduce the distance to the dispenser as the experiment progresses. Finally, Panel C shows recurrence plots. This plot depicts change of regions of each rat (in a matrixial configuration of 10 x 10 virtual zones) as the session progresses (see supplementary material). Both axes show time on a time frame of 0.2 s. If a rat was on a R_k region in a T time and on T+1 was on the same region, a black mark represented the recurrence in a given location time. If, on the contrary, on T+1 the rat was on a different location, a white mark would be shown. The densification and alternation of black-white mosaic patterns indicate high recurrence to a given region; a higher proportion of continuing black zones would mean higher permanence while a higher proportion of white zones would mean extended transitions among regions. Panel C shows a perspicuous difference between both conditions, higher recurrence under FT than in TV, and higher permanence in zones under VT than FT.

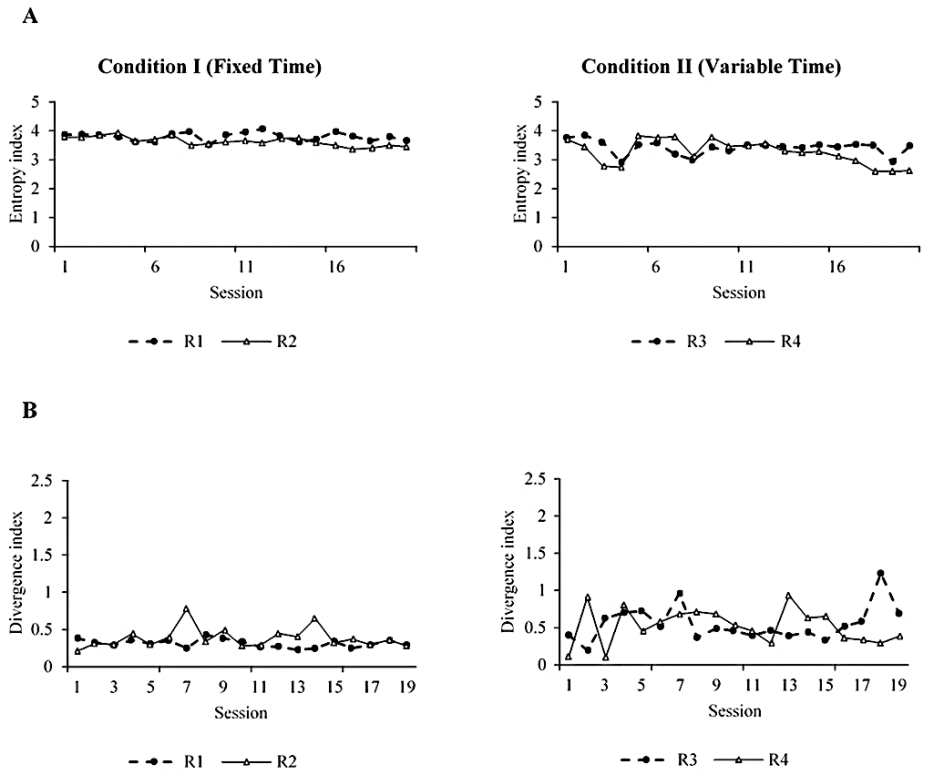

Figure 3. Entropy (Panel A) and Divergence (Panel B) measures for subjects R1 and R2 under Fixed Time schedules (left), and subjects R3 and R4 under Variable Time (right).

Figure 3 shows the entropy (Panel A) and divergence (Panel B) values per session for each rat for both conditions. The entropy is useful in the context of this experiment as a measure of variation of locomotion patterns and the dynamic of behaviour (see methodological and mathematical description in the supplementary material). For our subject matter, higher entropy represents high variation and dynamics of the spatial behaviour. In Panel A, the similarity between entropy plots within the condition and the difference between conditions are clear. The entropy was higher under FT than VT. In order to determine the variations of spatial behaviour between consecutive sessions, a divergence index was calculated (Panel B). This index was calculated by comparing the distribution of the locomotion of the organism into the arena between two consecutive complete sessions (e.g., 1 and 2; 2 and 3, etc.). A value close to zero indicates no difference in the distribution of locomotion between sessions; a value far from zero indicates a difference in the distribution of locomotion between complete sessions (see mathematical

description in supplementary material). Panel B shows that the divergence was lower and more stable under FT than VT, this implied more variation of spatial behaviour between consecutive sessions under VT.

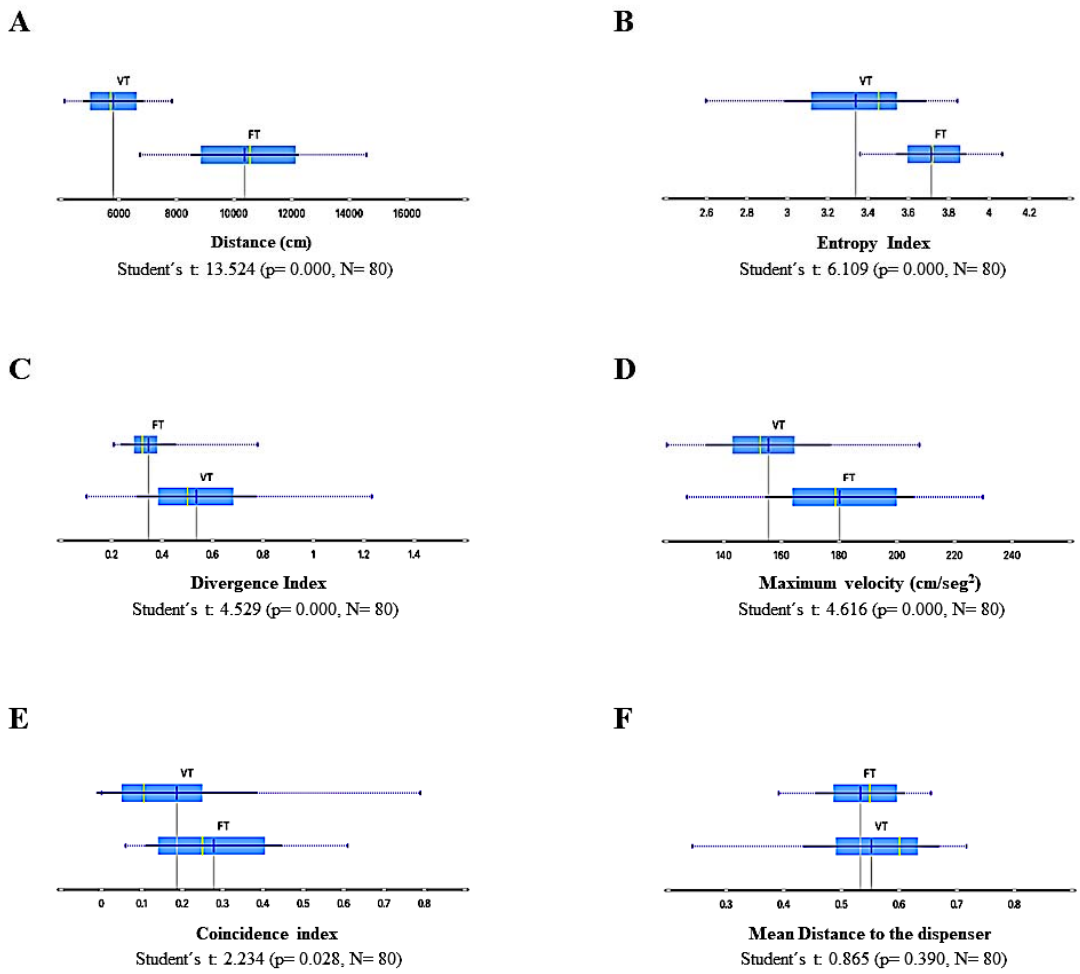

Figure 4. Summary results of spatial-behavior measures, for all sessions and subjects under Fixed Time (FT) and Variable Time (VT) schedules. Panel A, travelled distance per session; Panel B, entropy; Panel C divergence; Panel D, maximum velocity per session; Panel E, coincidence Index; and Panel F mean distance to the dispenser. Each box depicts the mean (dark blue vertical line), the median (yellow vertical line), the standard deviation (thin blue line) and the values between the first and the third quartile (blue highlighted area).

Figure 4 shows a summary results, of all sessions of the experiment for all subjects, of relevant measures related to the spatial dimension of behavior, of first and non-first order (entropy and divergence), and other measures of spatial behavior related to the dispenser and the time when water was available. The travelled distance per session (Panel A), entropy (Panel B) and maximum velocity in a given frame, per session (Panel D) were clearly higher under FT than VT, whereas the divergence (Panel C) was significantly higher under VT than FT. On the other hand, the mean distance to the water dispenser per session (Panel F) was more dispersed under VT than TF and slightly higher, but the difference between both conditions was not robust. Finally, the coincidence index (Panel E) of the location of the organism in the dispenser zone (10 cm radio around to the dispenser allocation) at the time when water was available (3 s) was higher under FT than VT. The coincidence index is relevant because it is closely related to measures of standard paradigms based on discrete and single response recording (e.g., entries to the dispenser).

In order to identify the relevance of each dimension or variable in the emergent behavioural system, understanding it as the functional interdependent relationship between variables concerning each condition, we conducted a *variable-ranking* analysis based on Machine Learning. The *variable-ranking* consists in a process of ordering a set of features by the value of a scoring function that measures the relevance of each feature according to a target as a predicting tool, in our case the experimental condition. *Variable-ranking* allows to know the importance or relevance of the features that better explain a target variable (for a complete description see supplementary material). Specifically, we used filter algorithms, the most used given the low computing resources used for applying them even on high dimensional datasets. Given our subject matter, the integrative analysis of spatial dynamics of behaviour with discrete responses under two different time-based schedules (FT vs VT) and our datasets, we applied three theoretical information filter algorithms for single *variable-ranking*, namely *information gain*, *mean decrease impurity Gini index* and χ^2 (for a complete description concerning to these algorithms see supplementary material), for *coincidence Index*, *mean distance to the dispenser*, *traveled distance*, *maximum velocity*, *entropy* and *divergence.*

	#	Info. gain	Gini	χ^2
N Trav Dist		0.766	0.410	48.133
N Entropy		0.276	0.172	22.533
N Divergence		0.248	0.157	17.633
N Max Vel		0.194	0.128	14.700
N Coinc Index		0.121	0.078	7.258
N Mean Dist to Disp		0.079	0.052	2.700
N Session		0.000	0.000	0.000

Figure 5. Ranking variable analysis, under *information gain*, *mean decrease impurity Gini index* and χ^2 procedures, for the features: travelled distance per session (Trav Dist), entropy, divergence, maximum velocity per session (Max Vel), coincidence index (Coinc index), mean distance to the dispenser (Mean Dist to Disp) and session. The length of the bar ranks the features by the scoring value that measures the relevance of each feature to differentiate the behavioral-system as a function of a given time based-schedule (Fixed vs Variable Time).

Figure 5 shows that according to the *variable-ranking* procedures, the most relevant features were related to the spatial dimension of behaviour, these were *travelled distance*, *entropy* and *divergence*. On the other hand, the *coincidence index*, the most closely feature related to the measures of the standard paradigms based on discrete response recording, was significatively less relevant than the other features related to the spatial dimension of behaviour.

With the purpose of having a perspicuous representation that would allow to identify if the data, given its multiple dimensions, are articulated or grouped as a function of the kind of time-based schedule employed, we conducted t-distributed Stochastic Neighbor Embedding, t-SNE. t-SNE is a machine learning algorithm useful for visualization of high-dimensional datasets into a bidimensional or three-dimensional space. t-SNE performs a non-linear dimensionality reduction task for embedding datasets and obtaining low dimension transformations as result. Relations between high dimensional data, that might be impossible to observe due to the large number of variables, could be distinguished after transforming them into a space with reduced dimension by t-SNE. The

representation obtained by t-SNE is perspicuous because the data with similar values, given the multiple features or input variables taken as a whole, is simply closer to each other (in a low dimensional space, 2D or 3D) than data with dissimilar values (for a complete description of t-SNE see supplementary material).

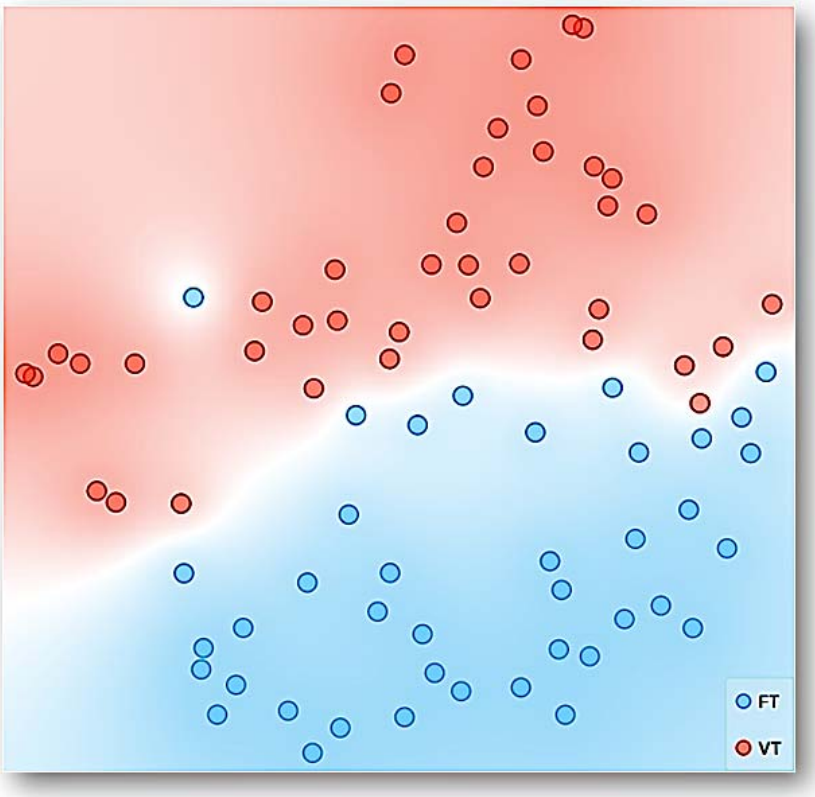

Figure 6. Representation with TSNE for the data of all experimental sessions and subjects. Each point represents a multidimensional data for a session, considering *distance travelled, entropy, divergence, maximum velocity, coincidence index, mean distance to the dispenser,* and *session number into the experiment* as dimensions, with time based-schedule, Fixed Time (FT) and Variable Time (VT), as a target feature. The data with similar values, given the multiple features or input variables taken as a whole, is simply closer to each other than data with dissimilar values.

Figure 6 shows a representation, using t-SNE, for the data of all experimental sessions and subjects. Each point could be seen as a multidimensional data for a session, considering the *distance travelled, entropy, divergence, maximum velocity, coincidence index, mean distance to the dispenser,* and *session number into the experiment* as dimensions, with condition, FT vs. VT, as target feature. FT data (blue points) tended to be

closer to each other, and the same was observed concerning VT data (red points). In order to facilitate the grouping visualization, color regions are shown in the figure. It is clear the conformation of only two predominant and well-delimitated regions, and the separation of FT and VT data, except for a few dots that are inserted in the colored region of the opposite condition. From this, it is plausible to assume that the multidimensional data had similar values within each condition in the multi-dimensional space, that given our subject matter represents the behavioural system, and dissimilar values between conditions.

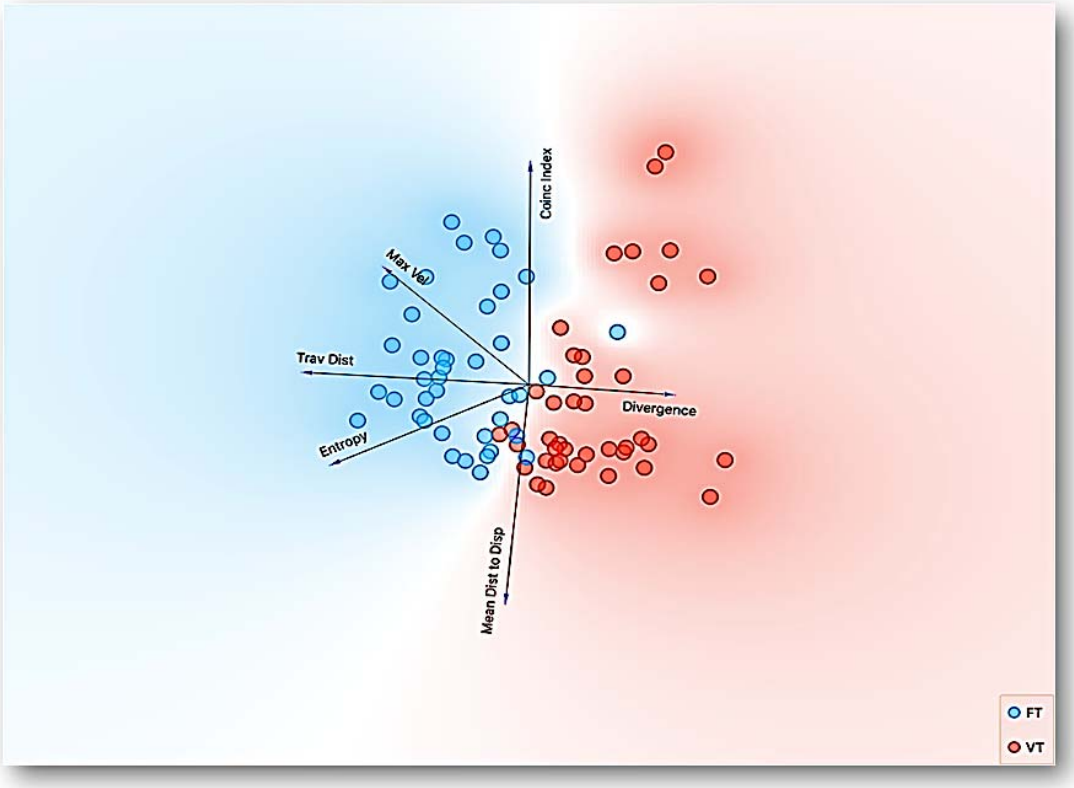

Figure 7. Representation with Linear Projection, by Principal Component Analysis, of multidimensional data of all sessions and subjects for six dimensions: *coincidence index*, *divergence*, *mean distance to water dispenser*, *entropy*, *travelled distance* and *maximum velocity*, with time based-schedule, Fixed Time (FT) and Variable Time (VT), as a target feature. The direction of each vector points out the direction to the increasing values for a given dimension, the allocation and the direction of the data within the projection show the tendency of the experimental condition data for each dimension.

Figure 7 shows the linear projection (for a full description see the supplementary material) of the multidimensional data of all sessions and subjects for six dimensions: *coincidence index*, *divergence*, *mean distance to water dispenser*, *entropy*, *travelled distance* and *maximum velocity*. The direction of each vector points out the direction to the increasing values for a given dimension, then the allocation and the direction of the data within the projection show the tendency of the experimental condition data for each dimension. In order to facilitate the visualization of the data tendency, colored regions related to each condition are added, the prevalence of a colored region in a given dimension represents higher values for the correspondent experimental condition to such color in comparison with the other experimental condition. So, the linear projection clearly showed higher values of *maximum velocity*, *travelled distance* and *entropy* for FT condition, while showed close values for *mean distance to the dispenser* for both conditions, but with a red shadow that suggests higher values for VT; on the other hand, the projection clearly showed higher values of *divergence* for VT, and close values for the *coincidence index* for both conditions, nevertheless de blue shadow in this last vector pointed out higher values for FT. One relevant difference of this representation with other reduction dimension procedures is that it has specifical representations for each relevant dimension of the data in the orthogonal space. The linear projection representation shows again the relevance of the spatial dimensions of behaviour related to the programmed time-based schedules.

Example 2

Motivational operations: Behavioral dynamics under different deprivations in concurrent schedules.

A procedure that is conducted in most studies of experimental analysis of behaviour that uses ‘appetitive’ stimuli, is the deprivation of a given commodity (e.g., water or food) that it is later used to be delivered contingent to some response or behavioural pattern in contingent schedules (Skinner, 1938)). Whereas in non-contingent schedules the delivery of such commodity is presented in conjunction with a given stimuli (e.g., pavlovian conditioning procedures) or it is simply presented according to a certain time rule (e.g., time-based schedules). The deprivation procedure, in methodological terms, has the purpose to establish the relevance or dispositional value of the delivered commodity as

stimuli (Michael, 1982; Reberg et al., 1978), in order to articulate behavioural patterns, responses and other stimuli (e.g., signal stimuli, discriminative stimuli, etc.) in a given function or behavioural system. The study of the relevance or dispositional value of a given stimuli, *por mor* of the deprivation operation, has been related to the field of motivation, under the terms of 'motivational operations' (Laraway et al., 2003), 'establishment operations' (Michael, 1982, 1993), among others.

Even though, a long time ago it was established that the ‘motivational’ function of a given stimulus (Duffy, 1951; 1957; Maier & Schneirla, 1964; Schneirla, 1959), in a non-mediational approach, could be characterized based on direction and vigor (or intensity) of the patterns implicated in the spatial dimension of behaviour, for the reasons exposed lines earlier in relation to recording and data analysis of the standard approach, the study of the dispositional value of a given stimulus (water or food), *por mor* of the 'motivational or establishment operations', have been restricted only to vigor or intensity of the discrete responses, and the spatial dimension of the behaviour and its dynamics has been ignored (e.g., Lewon et al. 2019).

On the other hand, generally, the effect of food or water deprivation is evaluated by removing access to them to the experimental subjects outside the experimental sessions and then presenting one or the other either contingent or noncontingent to a given response (Skinner, 1938; Bolles, 1975) during the session. The effect of presenting food and water concurrently when subjects are food or water deprived has been less studied (Fallon et al., 1965, Lewon et al. 2019). Under this rationale, the objective of this study was to evaluate the effects of food and water deprivation conditions on the behavioral continuum, integrated by the spatial dynamics of behavior and discrete responses, in conditions where food and water are concurrently delivered, from an multidimensional and multilevel analysis and data representation using machine learning tools.

Method

Subjects

Five female and one male (Subject 3) Wistar rats of approximately 5 months old at the beginning of the experiment. Rats were housed in individual home cages and placed on a water or food-restriction schedule, according to the current phase of the experiment, for

22 hrs before every experimental session. All procedures were conducted in agreement with university regulations of animal use and care and followed the official Mexican norm NOM-062-ZOO-1999 for Technical Specification for Production, Use and Care of Laboratory Animals.

Apparatus

An experimental chamber of 92 cm width x 92 cm long and 33 cm height was used. 2 cm above the grid floor and in the center of opposed walls two dispensers were located, a liquid dipper (Coulbourn E14-05,) and a modified food receptacle with a pellet dispenser (Coulbourn E14-24). The dipper allowed access to 0.1 cc of water for 3 s, while the pellet dispenser delivered a 45 mg. pellet with limited availability of 3 s. Entries to both dispensers were detected by Head Entry Detectors (MED ENV-254-CB). Above both dispensers a yellow light was used as visual stimulus (MED ENV-222M) to indicate food or water delivery (for a diagram of the apparatus see Hernández, León and Quintero, 2021). Water and food deliveries were programmed and registered with the Software MED PC IV, head entries were also registered using this software. Rat's displacement in the experimental chamber was registered using a video camera Topica TP-505D/3, which was 1 m above the chamber. The video camera was connected to a PC with software Ethovision 2.3. With this software were obtained records of rats' displacement in X, Y coordinates every 0.2 s.

Procedure

Experimental phase

After an initial training phase to the food and water dispenser (see Hernández et al for a complete description) subjects were exposed to two deprivation conditions: 1) Water-Deprivation (WD) and, 2) Food-Deprivation (FD). Each of them consisted of three days with the corresponding food or water restriction and one experimental session per day. After each condition, subjects were allowed unrestricted access to both commodities for 24 h before the next deprivation condition in order to avoid a drastic decrease in weight and to separate the effect of each deprivation (Lewon, et al., 2019). In order to control for the potential effect of the first deprivation condition on the subsequent condition, subjects were assigned to one of two deprivation sequences, the specific order of deprivations for each sequence is shown in Table 1. All experimental sessions consisted of presenting a CONC

FT 30 s FT 30 s schedule of food and water with limited availability of 3 s, a yellow light above both dispensers was turned on with every delivery and remained on for the 3 s of food or water availability. All experimental sessions lasted 30 min.

Table 1. Sequence of deprivation conditions for each group.

Sequence	Deprivation Condition	
1	WD	FD
2	FD	WD

Note. WD: Water Deprivation, FD: Food Deprivation. Each condition lasted 3 sessions and each session lasted 30 minutes. Three rats were assigned to Sequence 1 and three rats to Sequence 2.

Results

With the purpose to characterize the behavioural continuum and to compare the spatial dynamics of behaviour under water and food deprivation, we conducted a multilevel analysis. In the same way of Example 1, first, we show representative within-subject results of the behavioural continuum within session, for the initial, intermediate and last session of the experiment, for one representative subject. Second, we show summary results for measures based on spatial behaviour, of first and non-first order, and measures based in discrete response in relation with water and food dispensers. Third, we conducted a multidimensional analysis and integrative representations based on Machine Learning.

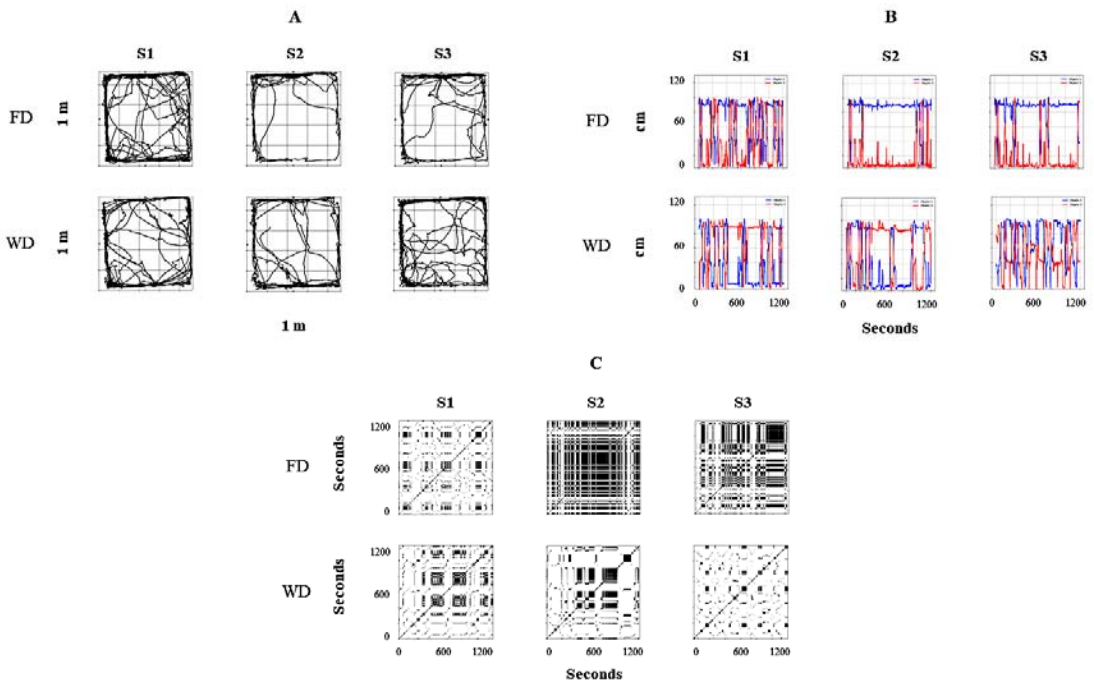

Figure 8. Representative within-subject results for all sessions of the behavioral continuum for one rat (R5). Each column depicts a session, and rows depict a deprivation conditions (FD and WD respectively). Panel A shows the routes of the rat in a bidimensional representation of the experimental chamber, red circle represents Food Dispenser location, blue circle represents Water Dispenser location; Panel B depicts the distance to the dispensers (Y axis) moment-to-moment (X axis), red line represents distance to Food Dispenser, blue line represents distance to Water Dispenser; and Panel C shows recurrence plots, this is change of regions of each rat (in a matrixial configuration of 10 x 10 virtual zones) as the session progresses.

Figure 8 shows the continuum spatial-behavioural data for the complete initial, intermediate and final sessions, for a representative experimental subject. Panel A represents the routes of the subject. For the intermediate and final sessions, there was a clear higher level of variation, extension and densification at the center zone of the arena under Water Deprivation (WD) than under Food Deprivation (FD); on the other hand, a higher densification in the food dispenser zone (top of the plot) under FD, and a distributed densification between both dispenser zones (top and down of the plot) under WD was observed. Panel B shows the distance to food dispenser (red line) and water dispenser (blue line), moment to moment (each .02 sec). For the intermediate and final sessions under FD, a small distance to the food dispenser, extended in time, and a long distance to the water

dispenser was observed, with only few alternations between high and low distance values to both dispensers. In contrast, under WD, for the intermediate and final sessions, a significant alternation between high and low values of distance to the dispensers and, then, a clear back and forth pattern between dispensers was observed. Panel C depicts the recurrence plots (for a complete explanation see Figure 2 description and supplementary material). In these plots, high permanence (extended black zones), with only some transitions, under FD and high recurrence (black-white mosaic patterns) under WD were observed. The three panels (A, B & C), as a whole, suggest a robust difference in the spatial dynamics by Food Deprivation vs Water Deprivation, under the same concurrent-schedule and for the same experimental subject.

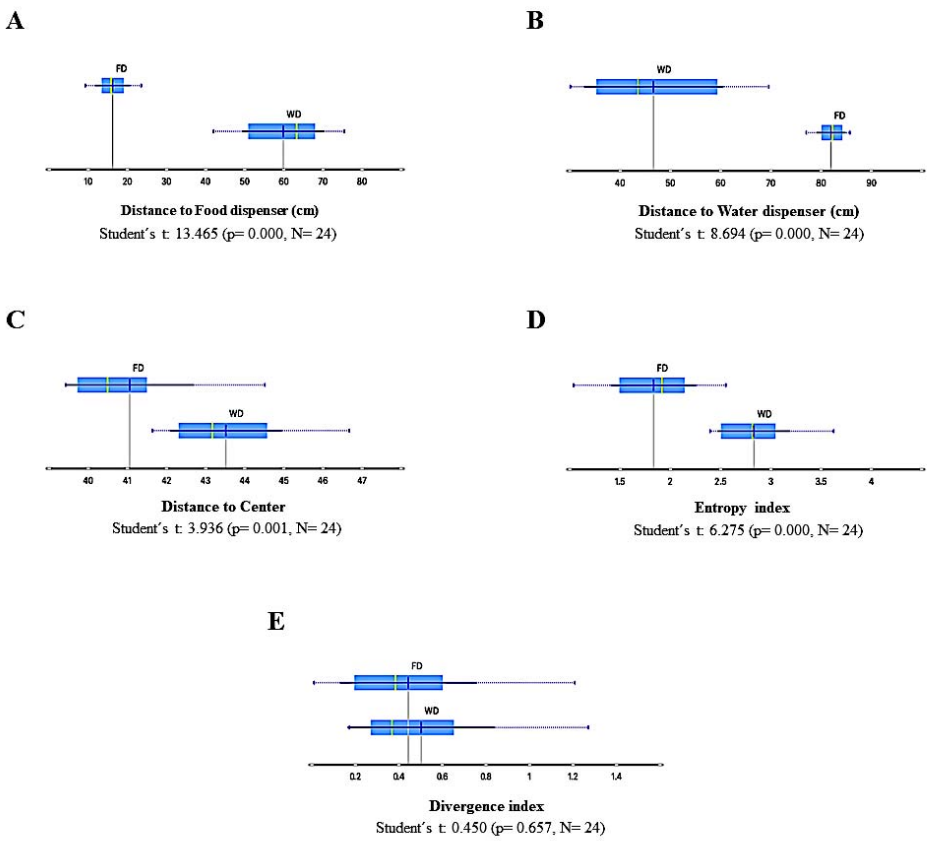

Figure 9. Summary results of spatial-behavior measures, for all sessions and subjects under Food Deprivation (FD) and Water Deprivation (WD) schedules. Panel A, Distance to food dispenser; Panel B, Distance to water dispenser; Panel C, Distance to center; Panel D, Entropy; Panel E, Divergence. Each box depicts the mean (dark blue vertical line), the median (yellow vertical line),

the standard deviation (thin blue line) and the values between the first and the third quartile (blue highlighted area).

Figure 9 shows summary results, for the measures based on the spatial dimension of behaviour: *mean distance to the food dispenser*, *mean distance to the water dispenser*, *mean distance to the center of the experimental arena*, *entropy index and divergence index*, under Food Deprivation (FD) and under Water Deprivation (WD), for all sessions and experimental subjects, independently of the sequence in which they were exposed. All measures were sensible to the deprivation condition, except the divergence index. The distance to the food dispenser had low values under FD and relatively high values under WD. The opposite effect concerning the water dispenser was observed, relatively low distance values under WD and high values under FD. The data of distance to the dispensers was more spread under WD than under FD. The mean distance to the center was higher under WD than FD, and the entropy index too. All the previously mentioned findings were very robust and point out a significant differential spatial dynamic of the behaviour related to both deprivation conditions.

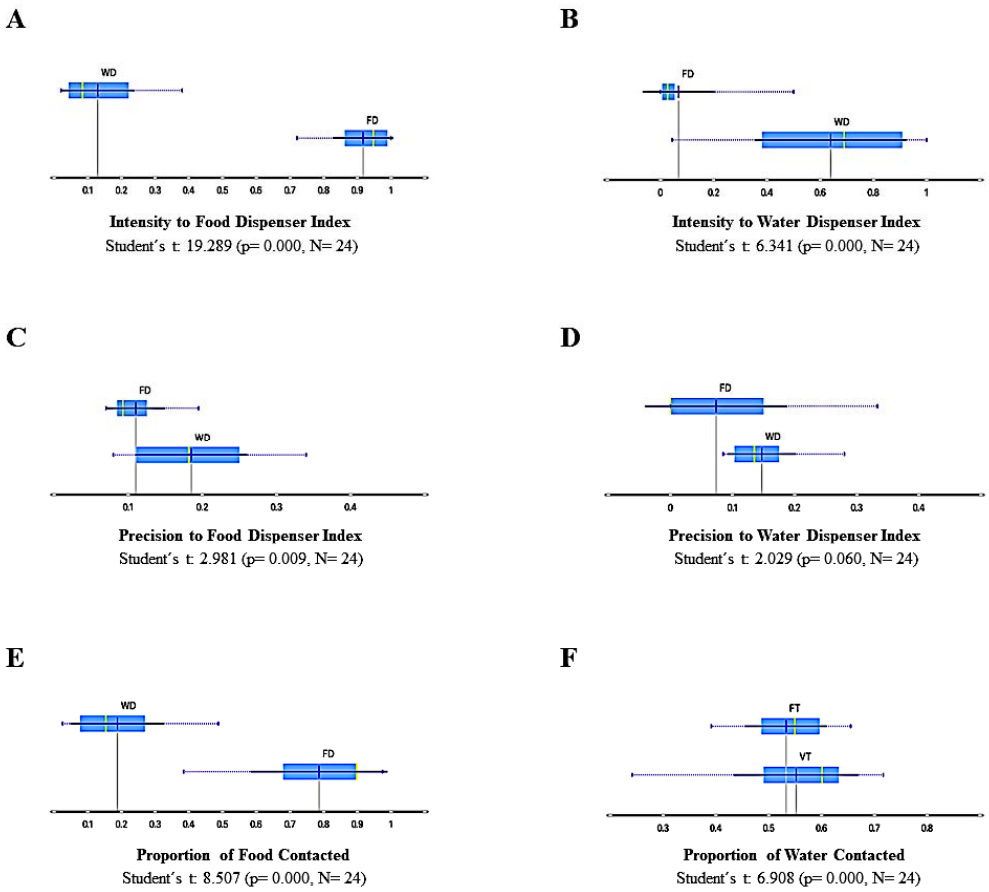

Figure 10. Summary results of measures based on discrete responses, for all sessions and subjects under Food Deprivation (FD) and Water Deprivation (WD) schedules, namely: Intensity to food dispenser index (Panel A), Intensity to water dispenser index (Panel B), Precision to food dispenser index (Panel C), Precision to water dispenser index (Panel D), Proportion of food contacted (Panel E) and Proportion of water contacted (Panel F). Each box depicts the mean (dark blue vertical line), the median (yellow vertical line), the standard deviation (thin blue line) and the values between the first and the third quartile (blue highlighted area).

Figure 10 shows a summary of results for measures based on discrete responses (entries into the dispenser and its relationship with food and water deliveries), namely, *intensity to food dispenser index*, *intensity to water dispenser index*, *precision to food dispenser index*, *precision to water dispenser index*, *proportion to food contacted* and *proportion of water contacted*. These measures are relevant because they are related to the ones employed in the standard paradigms based on single discrete responses. Panel A and

Panel B depict the intensity to the dispensers, the *intensity index* was obtained by dividing the total number of head entries in one dispenser of each session by the maximum number of entries in any session on the whole experiment for that particular subject and dispenser. Then this procedure was carried on for each subject and session always using this within-subject and within-dispenser comparison. The *intensity to food dispenser* was high under FD and low under WD, while the *intensity to water dispenser* was high, though spread, under WD and very low under FD. Panel C and Panel D show the precision to the dispensers. *Precision index* was obtained by dividing the number of entries when the commodity was available (water or food) to each dispenser on each session by the total number of head entries in that session and in that dispenser. In order to palliate *possible ceiling* or *floor effects* in sessions, the ratios that were obtained from sessions with total number of head entries that were below of percentile 5 of the data for each subject on each dispenser were eliminated. The *precision to food dispenser* was lower under FD than under WD, and there was no difference in precision to water dispenser between deprivations (FD and WD). Finally, Panel E and Panel F depict the proportion to food and water contacted from the total available. The *proportion to food contacted* was higher under FD than WD, while the *proportion to water contacted* was lower under FD than WD. The measures based on discrete responses, as a whole, show interesting findings, first the *intensity* and *effectiveness* (i.e., proportion to food contacted) to each dispenser clearly depend on the deprivation condition, this is, high values of intensity and effectiveness to food dispenser was observed under FD, and vice versa, high values of intensity and effectiveness to water dispenser was observed under WD. Nevertheless, the *modulating effect* of each deprivation condition over the behaviour related to the correspondent dispenser and commodity delivery to such deprivation is not exactly the same for both deprivations. On the one hand, the *modulating effect* of FD, for all behavioural measures based on discrete responses, are most robust for the food dispenser than the effect of WD over the same measures related to water dispenser. On the other hand, the data under FD tends to extreme values (very low or very high) related to *intensity* and *effectiveness*, while under WD tends to intermediate and spread values. Finally, it is remarkable that the precision of behaviour related to the food delivery was negatively affected under FD, and that this effect for water delivery under WD was not observed.

	#	Info. gain	Gini	χ^2
N Dist FDisp		1.000	0.500	16.000
N Dist WDisp		1.000	0.500	16.000
N Intensity FDisp		0.829	0.427	16.000
N Proportion FContacted		0.748	0.381	12.100
N Entropy		0.675	0.361	13.444
N Intensity WDisp		0.675	0.361	13.444
N Proportion WContacted		0.656	0.358	10.526
N Precision WDisp		0.568	0.289	5.121
N Dist Center		0.541	0.278	7.111
N Precision FDisp		0.209	0.134	5.444
N Divergence		0.041	0.028	0.111
N Session		0.000	0.000	0.000
C Sequence	2	0.000	0.000	0.000

Figure 11. Ranking variable analysis, under *information gain*, *mean decrease impurity Gini index* and procedures, for the features: Distance to food dispenser (Dist FDisp), Distance to water dispenser (Dist WDisp), Intensity to food dispenser (Intensity FDispenser), Proportion of food contacted (ProportionFContacted), Entropy, Intensity to water dispenser (Intensity WDisp), Proportion of water contacted (Proportion WContacted), Precision to water dispenser (Precision WDisp), Distance to the center of the experimental arena (Dist Center), Precision to food dispenser (Precision FDisp), Divergence, Session, Sequence.

Figure 11 shows the variable-ranking, under three procedures, namely *Information gain*, *impurity Gini index* and , for all measures, those based on continuum spatial dimension of behaviour and those based on discrete responses (for a complete description concerning to these algorithms see the supplementary material, and for a suggested use in behavior analysis see the description of Figure 5). The variable-ranking allows to identify the relevance of each variable (i.e., behavioural measure or dimension) into the whole multidimensional system. Given our subject matter, the modulating effect of two different deprivations (FD and WD) into the multidimensional behavioural system, the variable-ranking suggests that the most relevant variables were the distance to the dispensers,

intensity to the dispensers and entropy. These findings suggest that the spatial dimension of behaviour was at least as important as discrete responses into the behavioural systems that emerge by modulation under food deprivation and water deprivation.

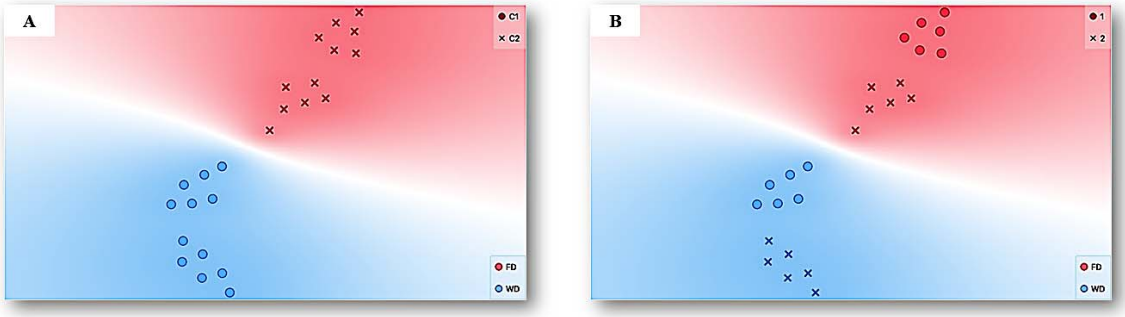

Figure 12. Representation with TSNE for the data of all experimental sessions and subjects. Each point represents a multidimensional data for a session, given all features (see Figure 11), with deprivation condition, Food Deprivation (FD-red) and Water Deprivation (WD-blue), as a target feature. The data with similar values, given the multiple features or input variables taken as a whole, is simply closer to each other than data with dissimilar values. Panel A, additionally, shows clustering under the K-means procedure and two well-delimitated colored regions, with a clear separation between FD and WD data, and corresponding each one with a cluster (C1 -circles- and C2 -crosses-). Panel B depicts, on the other hand, the deprivation sequence (Sequence1 -Circle- and Sequence2 -crosses-).

Figure 12 shows a representation by t-SNE (for a complete explanation see supplementary material and description of Figure 6) for the data of all the experimental sessions and subjects. Each point could be seen as a multidimensional data for a session, considering both measures based on the continuum spatial behaviour as those based on discrete responses (see Figure 11), and deprivation condition (FD and WD) as the target feature. FD data (red points) tend to be closer to each other, and the same is observed concerning WD data (blue points). Two well-delimitated colored regions, with a clear separation between FD and WD data, was conformed. Additionally, two clusters were conformed under the K-means clustering procedure (for a description see supplementary material), see Panel A. The coincidence of each cluster data with a deprivation condition

data was very robust. This complementary analysis could be taken as a clear confirmation of the differential modulation by each deprivation condition (FD vs WD) over the emerged multi-dimensional behavioural system under the same concurrent schedule and within-subject design. Finally, in Panel B, other complementary representation was conducted. In this panel, the circles point out the deprivation sequence 1 (WD-FD) and the crosses sign out the deprivations sequence 2 (FD-WD). The representation shows that the data clustering by deprivation was robust to the sequences (that is, there are well-delimited regions for each deprivation regardless of the sequence), but at the same time suggests that the data tended to be close by sequence, within deprivation. In addition, the representation suggests a *contrast effect* on deprivation conditions by Sequence 1, this is, the FD data and WD data were more distant from each other than the data for the same deprivation conditions in the Sequence 2.

Discussion

The purpose of the present work was threefold: 1) to propose an integrative and multidimensional approach for the analysis of behavioral systems; 2) to show novel behavioural aspects revealed under a multidimensional approach based on the integration of discrete and continuous data assisted by Machine Learning tools; and 3) to provide relevant and novel behavioural measures and data representations based on the integration of spatial dynamics and discrete responses, for the study of behavioural systems related to relevant research areas in behavioural science such as *water-seeking behaviour* and *motivational operations*.

The proposed approach showed to be useful to integrate a multiple-level analysis, to coalesce discrete and continuous dimensions of behaviour (and derivate measures of first and non-first order) as a whole system. It also proved to be fruitful to provide a broad characterization of the continuum of behaviour in which the spatial dynamics are on the first plane. The proposed approach appears promising to characterize and integrate different behavioural qualities pointed as relevant throughout the development of behavioural science, related with direction (Schneirla, 1959; in our work distance to the dispenser), vigour (Duffy, 1957; in our work speed, acceleration), variation (Antonitis, 1951; Berlyne, 1955; Iversen, 2017; Mowrer & Jones, 1943; in our work entropy), preference (Irwin, 1958; in our work time spent in zone), persistence (Bolles, 1975; in our work dispenser entries),

among others, as a complete behavioural system. So, with the proposed multidisciplinary methodological approach, the purpose of overcoming the segmented characterization of the behavioural continuum and its derived paradigms, for example the single response paradigm (Henton & Iversen, 1978), could go beyond the theoretical level that has been maintained up to now (Kantor, 1958).

The findings of both experiments, presented to exemplify our approach, show that the recording and analysis of the continuum of spatial-behaviour of the organisms is of primary importance to account for the principles that underlie in behavioural systems, and suggest that: a) moment-to-moment analysis and representations of locomotion-based data, across complete sessions, are useful to identify, and characterize, the behavioral dynamics under different stimuli-schedules and deprivation conditions (see *routes*, *distance to the dispensers* and *recurrence plots*); b) the proposed non-first order variables (i.e. *entropy* and *divergence*), based on locomotion data, are relevant and sensible to stimuli-schedule and deprivation conditions; c) the variables based on locomotion-data could be more sensible, than variables based on discrete responses, to stimuli schedules and deprivation conditions (see *variable-ranking* analysis based on Machine Learning); d) discrete responses and the continuum of spatial behaviour comprise an unitary and whole system, that could be apprehend and represent, in a perspicuous way, with Machine Learning tools like *t-SNE*, *clustering* based on *K-means*, *linear projection*, among others.

The experiments and its findings suggest that the proposed multidisciplinary methodological-approach allows going forward on the explanation of behavioural systems and reveals an integration of spatial-dynamics and discrete responses, related to water-seeking behaviour (Leon, et al., 2020a) and motivational operations (Hernandez, et al., 2021; Michael, 1982, 1993) under temporally based stimuli-schedules, hidden until now for the behavioural science.

Although the proposed approach appears to be promising, in order to confirm its heuristic and parsimonious value, it should be evaluated under a) other relevant phenomena; b) other kind of schedules (e.g., contingent schedules); c) different stimulating conditions (e.g., aversive stimulation); d) different organization of behavior (e.g., behavior under stimulus control; relational behavior); e) different species, including humans.

Finally, the proposed approach could be strengthened with the Integration of additional first and non-first order measures, pertinent to apprehend and characterize the dynamics of relevant dimensions of behavior (such as direction, variation, vigor, among others). On the other hand, additional Artificial Intelligence tools, like predictive analysis, could be explored in order to extend the scope of our approach for the behavioral science, and specifically for the experimental analysis of behavior.

As a corollary, the fast-paced development of contemporary computational tools, of fields as Artificial Intelligence, have rapidly change the landscape of some fields of behavioral science in the last decades, for example, ethology (Dell, et al., 2014) and neuroscience (Datta, et al., 2019; Mathis, et al., 2019; Mathis & Mathis, 2020; Wiltschko et al, 2015). It is time that the non-mediational, systematic, parametric (Henton & Iversen, 1975; Schoenfeld & Cole, 1972; Skinner, 1938) and ecological (Silva & Timberlake, 1997; Timberlake, 1994) approaches in the experimental analysis of behaviour start to profit from these tools (Turgeon & Lanovaz, 2020).

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

References

Antonitis, J. J. (1951). Response variability in the white rat during conditioning, extinction, and reconditioning. *Journal of Experimental Psychology*, *42*(4), 273-281. https://doi.org/10.1037/h0060407

Baum, W. M., & Rachlin, H. C. (1969). Choice as time allocation 1. Journal of the experimental analysis of behavior, 12(6), 861-874. https://doi.org/10.1901/jeab.1969.12-861

Berlyne, D. E. (1955). The arousal and satiation of perceptual curiosity in the rat. *Journal of Comparative and Physiological Psychology*, *48*(4), 238. https://doi.org/10.1037/h0042968

Bolles, R. C. (1975). *Theory of motivation*. HarperCollins Publishers.

Boren, J. J., Moerschbaecher, J. M., & Whyte, A. A. (1978). Variability of response location on fixed-ratio and fixed-interval schedules of reinforcement. *Journal of the Experimental Analysis of Behavior, 30(1), 63–67.* https://doi.org/10.1901/jeab.1978.30-63

Datta, S. R. (2019). Q&A: Understanding the composition of behavior. *BMC biology*, *17*(1), 1-7. https://doi.org/10.1186/s12915-019-0663-3

Datta, S. R., Anderson, D. J., Branson, K., Perona, P., & Leifer, A. (2019). Computational neuroethology: a call to action. *Neuron*, *104*(1), 11-24. https://doi.org/10.1016/j.neuron.2019.09.038

Dell, A. I., Bender, J. A., Branson, K., Couzin, I. D., de Polavieja, G. G., Noldus, L. P., ... & Brose, U. (2014). Automated image-based tracking and its application in ecology. *Trends in ecology & evolution*, *29*(7), 417-428. https://doi.org/10.1016/j.tree.2014.05.004

Drew, M. R., Zupan, B., Cooke, A., Couvillon, P. A., & Balsam, P. D. (2005). Temporal Control of Conditioned Responding in Goldfish. *Journal of Experimental Psychology: Animal Behavior Processes*, 31(1), 31–39. https://doi.org/10.1037/0097-7403.31.1.31

Duffy, E. (1951). The concept of energy mobilization. *Psychological Review*, *58*(1), 30. https://doi.org/10.1037/h0054220

Duffy, E. (1957). The psychological significance of the concept of" arousal" or" activation.". *Psychological review*, *64*(5), 265-275. https://doi.org/10.1037/h0048837

Escobar, R. (2014). From relays to microcontrollers: The adoption of technology in operant research. *Revista Mexicana de Análisis de la Conducta*, *40*(2), 127-153. http://dx.doi.org/10.5514/rmac.v40.i2.63673

Fallon, D., Thompson, D. M., & Schild, M. E. (1965). Concurrent food-and water-reinforced responding under food, water, and food-plus-water deprivation. *Psychological Reports*, *16*(3_suppl), 1305-1311. https://doi.org/10.2466/pr0.1965.16.3c.1305

Ferster, C. B., & Skinner, B. F. (1957). Schedules of reinforcement. https://doi.org/10.1037/10627-000

Gibson, J. J. (1979). *The ecological approach to visual perception*. Boston, MA, US: Mifflin and Company. https://doi.org/10.1002/bs.3830260313

Henton, W. W., & Iversen, I. H. (1978). Classical and operant conditioning: a response pattern analysis. https://doi.org/10.1007/978-1-4612-6310-4

Hernandez, V., León, A., & Quintero, V. (2021). Food and water deprivation modulating function on activation and direction of behavior in Wistar rats. https://doi.org/10.31234/osf.io/234sh

Irwin, F. W. (1958). An analysis of the concepts of discrimination and preference. *The American Journal of Psychology*, *71*(1), 152-163. https://doi.org/10.2307/1419203

Iversen, I. H. (2017). An inexpensive method to study response variability in acquisition and extinction of operant behavior. *Revista Mexicana de Análisis de la Conducta*, *43*(2), 212-241. https://doi.org/10.5514/rmac.v43.i2.62314

Kantor, J. R. (1970). An analysis of the experimental analysis of behavior (TEAB). *Journal of the Experimental Analysis of behavior*, *13*(1), 101. https://doi.org/10.1901/jeab.1970.13-101

Kantor, J. R. (1958). Interbehavioral psychology: A sample of scientific system construction.

Kuo, Z. Y. (1976). *The dynamics of behavior development: an epigenetic view*. Plenum.

Lachter, G. D., Cole, B. K., & Schoenfeld, W. N. (1971). Response rate under varying frequency of non-contingent reinforcement. *Journal of the Experimental Analysis of Behavior*, 15(2), 233–236. https://doi.org/10.1901/jeab.1971.15-233

Laraway, S., Snycerski, S., Michael, J., & Poling, A. (2003). Motivating operations and terms to describe them: Some further refinements. *Journal of applied behavior analysis*, *36*(3), 407-414. https://doi.org/10.1901/jaba.2003.36-407

León, A., Hernandez, A. V., Huerta, U., Hernandez, C. A., Toledo, P., Avendaño, M. L., ... & Guzmán, I. (2020a). Ecological location of a water source and spatial dynamics of behavior under temporally scheduled water deliveries in a modified open field system: An integrative approach. *Frontiers in psychology*, *11*, 3477. https://doi.org/10.3389/fpsyg.2020.577903

León, A., Tamayo Tamayo, J., Hernández Eslava, V., Toledo Hernández, P., Avendaño Garrido, M. L., Hernández Linares, C. A., & Escamilla Navarro, E. (2020b). Motus:

software for the behavioral analysis of displacement patterns. *Mexican Journal of Behavior Analysis*, *46*(1). http://dx.doi.org/10.5514/rmac.v46.i1.76960

Lewon, M., Spurlock, E. D., Peters, C. M., & Hayes, L. J. (2019). Interactions between the effects of food and water motivating operations on food□and water□reinforced responding in mice. *Journal of the experimental analysis of behavior*, *111*(3), 493-507. https://doi.org/10.1002/jeab.522

Loveless, J., Webb, B. Chaotic worms. *Nat. Phys.* 17, 170–171 (2021). https://doi.org/10.1038/s41567-020-01058-2

Maekawa, T., Ohara, K., Zhang, Y., Fukutomi, M., Matsumoto, S., Matsumura, K., ... & Yoda, K. (2020). Deep learning-assisted comparative analysis of animal trajectories with DeepHL. *Nature communications*, *11*(1), 1-15. https://doi.org/10.1038/s41467-020-19105-0

Maier, N. & Schneirla, T. (1964). *Principles of Animal Psychology*. New York, U.S.A: Dover Publications Inc.

Marshall, J. D., Aldarondo, D. E., Dunn, T. W., Wang, W. L., Berman, G. J., & Ölveczky, B. P. (2020). Continuous Whole-Body 3D Kinematic Recordings across the Rodent Behavioral Repertoire. *Neuron*. https://doi.org/10.1016/j.neuron.2020.11.016

Mathis, A., Mamidanna, P., Cury, K. M., Abe, T., Murthy, V. N., Mathis, M. W., & Bethge, M. (2018). DeepLabCut: markerless pose estimation of user-defined body parts with deep learning. *Nature neuroscience*, *21*(9), 1281-1289.https://doi.org/10.1038/s41593-018-0209-y

Mathis, A., Pack, A. R., Maeda, R. S., & McDougle, S. D. (2019). Highlights from the 29th Annual Meeting of the Society for the Neural Control of Movement. https://doi.org/10.1152/jn.00484.2019

Mathis, M. W., & Mathis, A. (2020). Deep learning tools for the measurement of animal behavior in neuroscience. *Current opinion in neurobiology*, *60*, 1-11. https://doi.org/10.1016/j.conb.2019.10.008

Michael, J. (1982). Distinguishing between discriminative and motivational functions of stimuli. *Journal of the experimental analysis of behavior*, *37*(1), 149-155. https://doi.org/10.1007/BF03392623

Michael, J. (1993). Establishing operations. *The behavior analyst*, *16*(2), 191-206. https://doi.org/10.1901/jeab.1982.37-149

Mowrer, O. H., & Jones, H. M. (1943). Extinction and behavior variability as functions of effortfulness of task. *Journal of Experimental Psychology, 33*(5), 369–386. https://doi.org/10.1037/h0056182

Pérez-Escudero, A., Vicente-Page, J., Hinz, R. *et al.* idTracker: tracking individuals in a group by automatic identification of unmarked animals. *Nat Methods* 11, 743–748 (2014). https://doi.org/10.1038/nmeth.2994

Reberg, D., Mann, B. & Innis, N. (1977). Superstitious behavior for food and water in the rat. *Physiology & Behavior*, 19(6), 803-806. https://doi.org/10.1016/0031-9384(77)90318-3

Reberg, D. Mann, B., Innis, N. & Eizenga, C. (1978). 'Superstitious' behaviour resulting from periodic response-independent presentations of food or water. *Animal Behaviour*, 26, 507-519. https://doi.org/10.1016/0003-3472(78)90067-2

Reynolds, G. S. (1975). *A primer of operant conditioning* (Rev. ed.). Scott, Foresman.

Sanabria, F., Thrailkill, E.A. & Killeen, P.R. Timing with opportunity cost: Concurrent schedules of reinforcement improve peak timing. *Learning & Behavior* 37, 217–229 (2009). https://doi.org/10.3758/LB.37.3.217

Schneirla, T. C. (1959). *An evolutionary and developmental theory of biphasic processes underlying approach and withdrawal*. In M. R. Jones (Ed.), *Nebraska symposium on motivation, 1959* (p. 1–42). Univer. Nebraska Press.

Schoenfeld, W. N., & Cole, B. K. (1972). *Stimulus Schedules: The T-[tau (romanized Form)] Systems*. HarperCollins Publishers.

Silva, K. M., & Timberlake, W. (1997). A behavior systems view of conditioned states during long and short CS–US intervals. *Learning and Motivation*, *28*(4), 465-490. https://doi.org/10.1006/lmot.1997.0986

Skinner,B. F. (1948). Superstition in the pigeon. *Journal of Experimental Psychology: General*,38,168–172. https://doi.org/10.1037/h0055873

Skinner, B. F. (1938). The behavior of organisms: an experimental analysis. Appleton-Century.

Timberlake, W. (1994). Behavior systems, associationism, and Pavlovian conditioning. *Psychon Bull Rev* 1, 405–420 (1994). https://doi.org/10.3758/BF03210945

Torabi, R., Jenkins, S., Harker, A., Whishaw, I. Q., Gibb, R., & Luczak, A. (2020). Application of deep neural network reveals novel effects of maternal pre-conception exposure to nicotine on rat pup behavior. *bioRxiv*. https://doi.org/10.1101/2020.07.16.206961

Turgeon, S., & Lanovaz, M. J. (2020). Tutorial: Applying machine Learning in behavioral research. *Perspectives on Behavior Science*, *43*(4), 697-723. https://doi.org/10.1007/s40614-020-00270-y

Turvey, M. T. (2018). *Lectures on perception: An ecological perspective*. Routledge.

Wiltschko, A. B., Johnson, M. J., Iurilli, G., Peterson, R. E., Katon, J. M., Pashkovski, S. L., ... & Datta, S. R. (2015). Mapping sub-second structure in mouse behavior. *Neuron*, *88*(6), 1121-1135. https://doi.org/10.1016/j.neuron.2015.11.031

Zuriff, G. E. (1970). A comparison of variable-ratio and variable-interval schedules of reinforcement. *Journal of the Experimental Analysis of Behavior*, 13(3), 369–374. https://doi.org/10.1901/jeab.1970.13-369