Approximations of Algorithmic and Structural Complexity Validate Cognitive-behavioural Experimental Results

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Abstract

We apply methods for estimating the algorithmic complexity of sequences to behavioural sequences of three landmark studies of animal behavior each of increasing sophistication, including foraging communication by ants, flight patterns of fruit flies, and tactical deception and competition strategies in rodents. In each case, we demonstrate that approximations of *Logical Depth* and *Kolmogorv-Chaitin*

complexity capture and validate previously reported results, in contrast to other measures such as Shannon Entropy, compression or ad hoc. Our method is practically useful when dealing with short sequences, such as those often encountered in cognitive-behavioural research. Our analysis supports and reveals non-random behavior (*LD* and *K* complexity) in flies even in the absence of external stimuli, and confirms the "stochastic" behaviour of transgenic rats when faced that they cannot defeat by counter prediction. The method constitutes a formal approach for testing hypotheses about the mechanisms underlying animal behaviour.

Keywords: behavioural biases; ant behaviour; Drosophila behaviour; rodent behaviour; communication complexity; tradeoffs of complexity measures; Shannon Entropy; Kolmogorov-Chaitin complexity; Bennett's Logical Depth.

Author Summary

Behavioural sequences consist of a finite number of actions or decisions combined in a variety of spatial and temporal patterns that can be analysed using mathematical tools. Understanding the mechanisms underlying complex human and animal behaviour is key to understanding biological and cognitive causality. In the past mathematical tools for the study of behavioural sequences had largely been drawn from classical probability theory and traditional information theory. Here we move several steps forward towards the use of more powerful mathematical tools drawn from algorithmic information theory with which to study and quantify the complex nature and underlying possible algorithmic mechanisms of animal behaviour. We introduce methods and a unifying framework based upon algorithmic information theory and apply it to 3 case studies producing landmark results in behavioural science related to the way in which ants, flies and rats behave when faced with environments of different complexity. A major aim of the paper is to get life scientists to use and exploit these tools.

Introduction

Since the emergence of the Bayesian paradigm in cognitive science, researchers have expressed the need for a formal account of 'complexity', and the need for help in arriving at objective interpretations of data from animal experiments. (e.g. Rushen, 1991; Manor 2013). They have, however, struggled to provide formal, normative, non ad-hoc and universal accounts of features in behavioural sequences that are more advanced than probabilistic tools. Algorithmic Information theory can provide measures for the high order characterisation of processes produced by deterministic choices which display no statistical regularities, and rankings of ordered versus random-looking sequences in terms of their information content and structural sophistication (amount of computation engaged in by a human or animal in decision making). Despite some measures of *fractality* and Shannon Entropy introduced previously in applications of relevance to human and animal behaviour (Sabatini, 2000; Rutherford et al., 2001; Costa et al., 2002; Maria et al. 2004; Manor 2012), little, if anything, has been numerically attempted towards a systematic animal behavioural analysis using measures of an algorithmic nature.

Among the diverse areas of behavioural science that may need novel algorithmic complexity measures, beyond classical probability, are the fields of probabilistic reasoning and animal behaviour. The famous work of Kahnemann, Slovic and Tversky (1982) aimed at understanding how people reason and make decisions when confronted with uncertain and noisy information sources. For example, people tend to claim that the sequence of heads or tails "HTTHTHHHHTT" is more likely to appear than the series "HHHHHTTTTT" when a coin is tossed. However, the probability of each string is $1/2^{10}$, exactly the same, as indeed it is for all strings of the same length. In the "heuristics and bias" approach advocated by Kahneman and Tversky (1982), these systematic errors were interpreted as biases inherent to human psychology, or as the result of using faulty heuristics. For instance, it was believed that people tended to say that "HHHHHTTTTT" was less random than "HTTHTHHHTT" because they were influenced by a so-called representativeness heuristic, according to which a string is more random the better it conforms to prototypical examples of random strings. Human reasoning, it was argued, worked like a faulty computer. Here we will suggest the opposite: that in light of modern research, these behavioural biases can be accounted for by powerful complexity measures that point towards an algorithmic basis for behaviour, a suggestion that accords with the results reported by some animal behaviour researchers (Ryabko and Reznikova 2009, Maye et al., 2007), and that implies that, rather than working like a faulty

computer, the brain actually has a purely algorithmic bias. Indeed, during the last few decades, a paradigm shift has occurred in cognitive science. The "new paradigm" suggests that the human (and animal) mind is not a faulty machine, but a probabilistic one, which we use to estimate and constantly revise probabilities of events in the world, taking into account previous information and computing possible models of the future. We also think the brain approximates rather than implements Bayesian computations (Marshall et al., 2013). One problem is how to build a prior that is at the same time neutral, making the fewest assumptions (Ockham's razor) while also taking into account all possible scenarios (Epicurus' Principle of Multiple Explanations), and being informative enough beyond statistical uniformity (Gauvrit et al., 2015).

Kolmogorov complexity (K) is meant to provide a way of dealing with these principles, and introduces another dimension to data analysis by quantifying simplicity versus randomness and separating correlation from causation. Kolmogorov complexity quantifies the complexity of an object by the length of its shortest possible description. For example, low K means that digits in a sequence can be deterministically generated---therefore each bit is causally connected by a common generating source. However, that a sequence has a large Shannon Entropy means that its digits do not look statistically similar, not that they are necessarily causally disconnected (e.g. 1, 2, 3, 4, 5...). Thus far, lossless compression algorithms have been commonly used to approximate Kolmogorov complexity. However, they are based on statistical properties of sequences that are used to encode regularities, and as such they are in fact Shannon Entropy rate estimators. Here we use an alternative method to approximate K based on Algorithmic Probability (Zenil & Delahaye, 2011; Soler-Toscano et al., 2014), a method that, unlike lossless compression (Cilibrasi, 2005), can also deal with short sequences typically encountered in the behavioural sciences. The same method will also serve to estimate Logical Depth (LD) (Bennett 1998) for these sequences, this is a measure that distinguishes structural complexity from randomness, something that Kolmogorov complexity does not by itself. The results reported here not only point us in this direction, unveiling some mechanisms that animals seem to use to cope with complexity in their environments, while also showing how they embrace it and even harness it.

Methods

The algorithmic theory of information provides a formal framework for describing intuitive notions of complexity. The algorithmic probability of a sequence s is the probability that a randomly chosen program running on a Universal (prefix-free) Turing Machine will produce s and halt. Since Turing Machines are conjectured to be able to perform any algorithmically-specified computation, this corresponds with the probability that a random computation will produce s. It therefore serves as a natural formal definition of a prior distribution for Bayesian applications. Also, as we will see in the next section, the algorithmic probability of a string s is negatively linked to its (Kolmogorov-Chaitin) algorithmic complexity, defined as the length of the shortest program that produces s and then halts (Kolmogorov 1965; Chaitin 1969).

One important drawback of algorithmic complexity (which we will denote by K) is that it is not computable. Or more precisely, K is lower-semicomputable, meaning that it cannot be computed with absolute certainty but can be arbitrarily approximated from above. Indeed, for a long time lossless compression algorithms had been used to approximate K, but today there exist methods to approximate the algorithmic probability (Delahaye and Zenil, 2011), and thus K, of strings of any length, even short ones (c.f. next section), which has spurred a renewed interest in objective numerical approximations of behavioural sequences. One feature that has been the basis of a criticism of applications of K, is that K assigns the greatest complexity to random sequences. However, by introducing computational time, measures of "sophistication" assessing structure and assigning low complexity to randomness have been proposed. One of these measures is a seminal contribution by Charles Bennett (Bennett, 1988), itself based on Kolmogorov complexity and called Logical Depth. Here we also estimate Logical Depth to quantify the complexity of behavioural sequences, because it can provide further insight into another important aspect of animal behavior beyond the simplicity and randomness, namely, the "computational effort" that an animal may invest in behaving in a particular way.

Algorithmic probability

One widespread method has long existed for assessing Kolmogorov-Chaitin complexity, namely, lossless compression because the size of a compressed file provides an upper bound of its algorithmic complexity. If lossless compression algorithms are justified for approximating Kolmogorov complexity, it is only because compression is a sufficient test for non-randomness, but they clearly fail in the other direction, being unable to tell whether something is the result of or is produced by an algorithmic process (such as the digits of the mathematical constant π). That is, they cannot find structure other than simple repetition. Lossless compression algorithms are inappropriate for short strings (of, say, less than a few hundreds of symbols). For short strings, lossless compression algorithms often yield files that are longer than the strings themselves, because they have to include the decompression instructions, hence providing very unstable results that are difficult, if not impossible, to interpret (see Table 1). In cognitive and behavioural science, however, researchers usually deal with short strings of at most a few tens of symbols, for which compression methods are useless. This is one of the reasons behavioural scientists have long relied on tailor-made measures of complexity instead, because the aforementioned factors limit the applicability of lossless compression techniques for the approximation of complexity in behavioural sequences. But more important, implementations of lossless compression algorithms are currently Shannon Entropy rate estimators and their connection to Kolmogorov complexity is no better or different than the known connection between Shannon Entropy and Kolmogorov complexity.

In many ways, animal behaviour (including, notably, human behaviour) suggests that the brain acts as a compression device (see also Gauvrit et al., in press). For instance, despite our very limited memory, we can retain long strings if they have low algorithmic complexity (Gauvrit et al., 2014). However, prior to recent developments, the behavioural sciences also relied largely on a subjective and intuitive account of complexity. The *Coding theorem method* (Delahaye and Zenil, 2011; Soler-Toscano et al., 2013) was specifically designed to address this challenge. An implementation called ACSS (for Algorithmic Complexity for Short Strings) is freely available as an R-package (Gauvrit et al., 2015), and through an

online complexity calculator (http://www.complexitycalculator.com). The idea at the root of the *Coding theorem method* is the use of algorithmic probability as a means to estimate algorithmic complexity. The algorithmic probability of a string s is defined as the probability that a universal prefix-free Turing machine U will produce s and then halt. Formally (Levin, 1974),

(1)
$$m(s) = \sum_{U(p)=s} 1/2^{-|p|}$$

Then the algorithmic complexity of a string s is defined as the length of the shortest program p that, running on a universal prefix-free Turing machine U, will produce s and then halt. Formally (Kolmogorov, 1965; Chaitin, 1969),

(2)
$$K(s) = min\{|p|, U(p) = s\}$$

K(s) and m(s) both depend on the choice of the Turing machine U. Thus, the expression "the algorithmic complexity of s" is, in itself, a shortcut. For long strings, this dependency is relatively small. Indeed, the invariance theorem states that for any two universal prefix-free Turing machines U and U, there exists a constant c independent of s such that (Solomonoff, 1964; Kolmogorov, 1965; Chaitin, 1969)

(3)
$$|K_U(s) - K_{U'}(s)| < c$$

The constant c can be arbitrarily large. If one wished to approximate the algorithmic complexity of short strings, the choice of U is thus relevant. To overcome this inconvenience, we can take advantage of a formal link established between algorithmic probability and algorithmic complexity. The algorithmic coding theorem states that (Levin, 1974)

(4)
$$K_U(s) = -\log_2(m_U(s)) + O(1)$$

This theorem can thus be used to approximate K_U (s) through an estimation of m_U (s) where K_U and m_U are approximations of K and m obtained by using a "reference" universal Turing machine U. Instead of choosing a particular "reference" universal Turing machine and feeding it with programs, Delahaye and Zenil (2011) used a huge sample of small Turing machines running on blank tapes. By doing so, they produced a frequency output distribution similar to averaging the output for an input over a large number of Turing machines as an approximation to m(s). CTM(s) is then defined as $-log_2(m_E(s))$ by the algorithmic Coding theorem (eq. 4), where m E(s) is the obtained distribution from the small Turing

machines (Delahaye and Zenil 2011 and Soler-Toscano et al., 2014). The method is based in the beautiful relationship between the complexity of an object and the probability of the object be produced by a random computer program (a Turing machine) as formalised by Eq 4. The idea is that objects with low Kolmogorov complexity have shorter descriptions and are therefore more likely to occur by chance. Think of n digits of π in binary, they have a probability of $1/2^n$ to be produced by chance but a $1/2^{|p|}$ chance if produced by a computer program p that produces the digits of π . Because π has very short descriptions (short formulae) it is of low Kolmogorov complexity and remains almost the same for no matter how many n digits of π . It is clear then that |p| < n and that while n grows linearly |p| grows logarithmic at most.

To justify the method given the dependence on reference machine (that determines the constant in Eq. 3), CTM was thoroughly investigated under different formalisms and applications. It has been shown that CTM, as computed with different samples of small Turing machines, remains stable (Soler-Toscano et al., 2014; Gauvrit et al., 2014 and Zenil et al., in press). Also, several descriptions of Turing machines did not alter CTM (Soler-Toscano et al., 2013 and Soler-Toscano et al., 2014). Zenil et al. (2012) also showed that CTM based upon cellular automata was similar to CTM based on Turing machines discounting for string length correlations (both reference CA and TM machines determined by a quasi-lexicographical enumeration). On a more practical level, CTM is also validated by experimental results (Zenil et al. 2014; Gauvrit et al., 2015; Kempe et al., 2015; Zenil et al. in press, among others). For instance, CTM provides a good fit to phenomena such as human complexity perception (Gauvrit et al. 2014b). Moreover, the transition between the use of CTM and lossless compression algorithms is smooth, the two behaving similarly when the scope of string lengths overlap (Zenil et al., in press B).

Bennett's Logical Depth

As noted in the Introduction, a measure of the "sophistication" of a sequence can be arrived at by combining the notions of algorithmic complexity and computational time. According to the concept of Logical Depth (Bennett, 1988), the complexity of a string is best defined by the time that an unfolding

process takes to reproduce the string from its shortest description. The longer it takes, the more complex. Hence complex objects are those that can be seen as "containing internal evidence of a nontrivial causal history" (Bennett, 1998).

Unlike algorithmic complexity, which assigns a high complexity to both random and highly organised objects, placing them at the same level, Bennett's Logical Depth assigns a low complexity to both random and trivial objects. It is thus more in keeping with our intuitive sense of the complexity of physical objects, because trivial and random objects are intuitively easy to produce, lack a lengthy history, and unfold quickly. Bennett's main motivation was actually to provide a reasonable means for measuring the physical complexity of real-world objects. Bennett provides a careful development (Bennett 1988) of the notion of logical depth, taking into account near-shortest programs, not merely the shortest one, in order to arrive at a robust measure. For finite strings, one of Bennett's formal approaches to the logical depth of a string is defined as follows:

Let s be a string and d a significance parameter. A string's depth at some significance d, is given by

(5)
$$LD_d(s) = min\{T(p) : (|p| - |p'| < d) \text{ and } (U(p) = s)\},$$

where T(p) is the number of steps in the computation U(p) = s, and |p'| is the length of the shortest program for s, (thus |p'| is the Kolmogorov complexity K(s)). In other words, LDd(s) is the least time T required to compute s from a d-incompressible program s on a Turing machine s; that is, a program that cannot be compressed by more than a fixed (small) number of s bits (Bennett, 1998). For algorithmic complexity the choice of universal Turing machine is bounded by an additive constant (as shown by the Invariance theorem described in the previous section), while for Logical Depth it is bounded by a multiplicative factor (Bennett 1989). The simplicity of Bennett's first definition of Logical Depth (Bennett, 1988), independent of size significance, makes it more suitable for applications (Zenil and Delahaye, 2011), serving as a practical approximation to this measure via the decompression times of compressed strings. To this end it uses lossless compression algorithms, whose deviation from perfect compression is unknown (and cannot, in general, be known due to uncomputability results), to calculate size significance. This is because where LD is concerned, it is more interesting or practically more

relevant to consider the shortest time vis-à-vis a set of near-smallest programs rather than just a single, perhaps unrepresentative, time taken by the shortest program alone. We will denote by LD(s) a measure approximating the Logical Depth of a string s, with no recourse to the significance parameter and approximated by a powerful method, an alternative to lossless compression, explained in the next section.

Numerical estimation of algorithmic probability and K

We use the concept of algorithmic probability for the calculation of K (and LD) by application of the algorithmic Coding theorem. A sample of 2,836 x 10^9 random Turing machines is selected from a reduced enumeration of all 5-state 2-symbol Turing machines (Soler-Toscano et al., 2013), using the standard Turing machine formalism of the 'Busy Beaver' problem (Rado, 1962; Brady, 1983). The output of the sample returns the string produced by the halting machines, together with their runtimes and the instructions used by each Turing machine---all the necessary information to estimate both an algorithmic probability measure and Logical Depth by finding the smallest machine (for this Turing machine formalism) producing s prior to halting, as illustrated in Figure 1.

Unlike lossless compression algorithms used to approximate K, CTM constitutes a truly algorithmic approach to K, rather than a merely statistical one. This is because unlike lossless compression, CTM can find the computer programs that produce certain non-statistical algorithmic patterns (simple subsequences such as 1, 2, 3, 4, ... or the decimal expansion of the mathematical constant π) that may only look random to traditional lossless compression algorithms and Shannon Entropy but clearly are not.

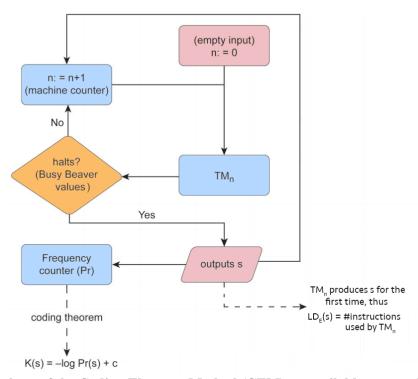


Figure 1 Flow chart of the Coding Theorem Method (CTM) --- available as a package (ACSS) in the R programming language --- shows how K and LD are approximated by way of an Algorithmic Probability-based measure upon application of the algorithmic Coding theorem for a fixed "natural" enumeration. An online tool that provides estimations of CTM, and soon will of BDM too, can be found at http://www.complexitycalculator.com

The flow chart in Figure 1 consists in running an enumeration of Turing machines and determining whether the machine halts or not for a large set of small Turing machines for which either their halting time can be decided (with the so-called Busy Beaver functions) or an educated theoretical and numerical guess made. The algorithm counts the number of times a sequence is produced, which is a lower bound on its algorithmic probability and then is transformed to an upper bound of the sequence's Kolmogorov complexity by means of the so-called algorithmic Coding theorem (bottom left). The same algorithm also finds the shortest, fastest Turing machine that produces the same sequence, hence providing an estimation of its Logical Depth (bottom right). The Block Decomposition Method (BDM) extends the range of application of CTM to longer strings by dividing and adding smaller pieces for which CTM has exact values (see Supplemental Material).

Application to data from animal behaviour experiments

To test the usefulness of algorithmic probability and logical depth for capturing intuitive notions of behavioural complexity, we applied these techniques to several experimental datasets for which complexity arguments are either lacking or have only been informally advanced. These datasets come from studies of the foraging behaviour of *Formica* ants in binary mazes (*e.g.* Reznikova, 1996), and of the flight behaviour of *Drosophila* flies in virtual arenas (*e.g.* Maye et al., 2007) and virtual competition experiments (Tervo et al., 2004).

Ant foraging and the complexity of instructions in binary mazes

In a well-known series of experiments (Reznikova, 1996), red-blood ant scouts (Formica sanguinea) and red wood ants (Formica rufa) were placed in a binary maze with food (sugar syrup) at randomly selected end points. Scout ants were allowed to return through the maze once they had found the food in order to communicate instructions to a foraging team from the colony; scout ants were claimed to translate sensorimotor experiences into numerical or logical prescriptions transmitted to conspecifics, in the form of sequences of branches (left or right) to follow in order to successfully find the food. 335 scout ants and their foraging teams took part in all the experiments with the binary tree mazes, and each scout took part in ten or more trials. 338 trials were carried out using mazes with 2, 3, 4, 5 and 6 forks. The scout ants were observed to take progressively longer to communicate paths in deeper mazes (with more turns); that is, they apparently transmitted more information. Informal results suggested that simpler instructions of "right" and "left" movements toward the food patches were communicated faster and more effectively than more complex (random-looking) behavioural sequences, thus suggesting that when strings are of the same length but transmitted at different rates, ants are capable of compressing the simpler sequences. When conducting the ant experiment, the researchers also found that almost all naive foragers were able to find food on their own, but that the time they spent was 10-15 times longer than the time spent by those ants that entered the maze after contact with a successful scout bearing information about the location of the food (Ryabko and Reznikova, 2009). Reznikova et al. (Ryabko and Reznikova, 2009; Reznikova and

Ryabko, 2011; Reznikova and Ryabko, 2012) and other researchers (Li and Vitanyi, 2008) were not able to numerically validate the relationship between complexity and communication times suggested by the results of the ant experiment. We applied our techniques for approximating algorithmic probability and logical depth (Delahaye & Zenil, 2012; Soler-Toscano et al., 2013) to these extant data, as described in detail in the Supplementary Information. As shown in Table 1 and Figure 2, independently of the validity of the original experiments, the claim related to the specific complexity of the behavioural sequences versus communication time is largely confirmed by the numerical estimations of the algorithmic complexity of the sequences by CTM.

Low random behaviour of fruitflies in the absence of stimuli

In another experiment, the behaviour of tethered flies was examined in a flight simulator consisting of a cylindrical arena homogeneously illuminated from behind (Maye et al., 2007). A fly's tendency to perform left or right turns (yaw torque) was measured continuously and fed into a computer. The flies were divided into three groups: the 'openloop' group flew in a completely featureless white panorama (*i.e.*, without any feedback from the uniform environment—open loop). In addition to the openloop group, data from two control groups were analysed. These groups flew in an arena that had either a single stripe ('onestripe' group) or was uniformly dashed ('uniform' group). The 'onestripe' group's environment contained a single black stripe as a visual landmark (pattern) that allowed for straight flight in closed-loop control, since the fly could translate its visual input into yaw torque to control the angular position of the stripe. The 'uniform' group flew in a uniformly textured environment that was otherwise free of any singularities; this environment was closed-loop in the same sense as that provided for the 'onestrip' group, since the fly could use its yaw torque to control the angular position of the uniform textured environment. Maye *et al.* (2007) concluded that in the featureless environment fly behaviour was non-random, with the distribution of yaw directions produced by flies in the 'openloop' group significantly deviating from the null Poisson distribution. As described in detail in the section headed Supplementary

Information, we applied our techniques to provide an algorithmic complexity and logical depth perspective on these data.

Animal behaviour in environments of increasing complexity

A virtual competitive setting was designed as described in Tervo et al. (2014). An algorithm playing the role of a virtual competitor (that can also be seen as a predator) against a rat was programmed to predict which hole (out of 2) the rat would choose against three increasingly complex predictive competitors. The rat had to choose a hole that it thinks will be not chosen by the competitor, in order to be rewarded. The task is therefore a prediction task, where the more successful the rat is at predicting the competitor's behaviour, the better it can avoid it and be rewarded. The first competitor consisted in an algorithm based on a binomial test able to react to significant bias. For example, if a rat had a clear predilection to choose either the left or right hole, Competitor 1 would correspondingly predict the hole with the statistical bias. Competitor 2, also based on a binomial test, reacts to any bias, and is therefore based upon a more sophisticated algorithm than Competitor 1 that makes Competitor 2 to perform in a less predictable fashion. Competitor 3 would, however, display a diverse range of features and therefore constitute a greater challenge to the rat. Each "environment" consisted in a long sequential list of trials for every competitor against 12 fresh individuals (rats) each time. Competitors 1 and 2 use conditional prevalence of the left and right choices, given a particular history pattern of up to three prior steps, to inform their prediction. The optimal deterministic strategy consists thus in keeping track of every pattern up to that length and ensuring that the conditional prevalence of going left or right is 0.5 (Tervo et al., 2014). The authors quantified how different the observed behaviour was from this optimal strategy by calculating the Kullback-Leibler divergence from the optimal---a variation of Shannon Entropy---of the observed distribution of conditional prevalences, given all small sequences of lengths n = 1, 2, and 3. Their results, backed by neural recordings based on the engagement of the anterior cingulate cortex, an area of the brain related to decision-making, showed that when rats are faced with competitors that they cannot outsmart, they switch from strategic counterprediction behaviour to a stochastic mode.

Results

K and LD estimations of animal behavioural sequences

The application of the algorithmic Coding theorem and the numerical estimates of Logical Depth provide objective quantification of animal behavioural sequences.

Ants' communication times follow complexity of foraging instructions

The order in which the behavioural sequences of ant turns by complexity (e.g. Reznikova, 1996) corresponds to an order of increasing Kolmogorov complexity, as approximated by algorithmic probability and logical depth, is shown in Table 1 together with comparisons with other measures in Figure 2. While we are not supporting or criticising the original results, using the tools introduced here to quantify the reported relationships, we arrived at the same conclusion that the authors put forward in connection to the communication and complexity tradeoff that was believed to take place. Table 1 and Figure 2 show that neither Entropy nor lossless compression (E, C and Bzip2) offer enough resolution to separate the complexity of behavioural sequences into more than 2 groups, because E counts the number of different symbols, and as said before current implementations of lossless compression (e.g. BZip2) are approximations to Entropy rate but also fail at compressing short strings. However, both CTM and LD are highly correlated, showing an increase in complexity as suggested by the authors of the original experiments. The same table also shows how lossless compression is traditionally unable to deal with short strings hence retrieving indistinguishable values among all cases.

Table 1. Movement and duration (as reported by Ryabko and Reznikova, 1996) of information transmission from F. sanguinea scouts to foragers; 0 encodes a right turn and 1 encodes a left turn in a binary maze. E(s) is the Shannon Entropy of s while CTM(s), C(s) and Bzip2(s) are all approximations to K(s), with CTM(s) the approximation to K(s) by Algorithmic Probability and C(s) and Bzip2(s) by lossless compression (Compress and BZip2). LD(s) is the approximation to Logical Depth by CTM. The table is sorted by duration.

Ant behavioural	Duration	E(s)	CTM(s)	C(s)	Bzip2(s)	LD(s)
sequence	(mean sec)	(bits)	(bits)	(bytes)	(bytes)	(number of instructions)

(turn pattern)						
110	69	0.636	6	64	37	3
11	72	0	3	64	37	2
000	75	0	4	64	37	3
111	84	0	4	64	37	3
00000	78	0	4	64	39	5
000000	88	0	5	64	39	7
111111	90	0	5	64	39	7
1011	100	0.562	6	64	37	4
0110	120	0.693	7	64	38	4
101010	130	0.693	8	64	37	7
010101	135	0.693	8	64	37	7
00101	150	0.673	7	72	37	5
010001	180	0.636	8	72	38	7
101101	200	0.636	8	64	38	7
001000	220	0.45	7	72	37	7

The (Pearson) correlations found among the values reported in Table 1 and plotted in Fig. 2 are as follows: Between the duration and Entropy the statistic was 0.616 with p-value 0.014. Between the duration and the estimation of Kolmogorov complexity (by CTM) the correlation was 0.82 with a p-value 0.00017; while for lossless compression (Compress) it was 0.61 with p-value 0.014, and (BZip2) 0 with p-value 1. The correlation between the duration of the ant communication and the estimation of Logical Depth was 0.75, with a p-value of 0.0013. The best--and highly significant--correlation was thus found between duration and Kolmogorov complexity estimated by CTM and Logical Depth. This formalises results previously based only upon visual inspection, intuition and traditional statistics, namely, that ant communication is correlated to the complexity of the instructions, i.e., instructions that take less time to communicate have low Kolmogorov complexity, while less efficiently communicated instructions have both higher K and higher LD.

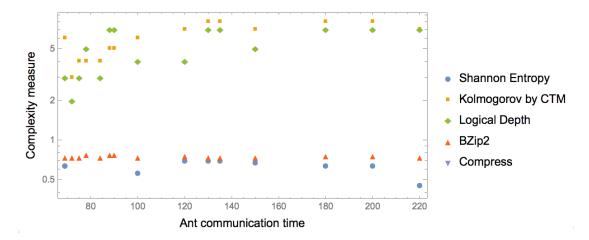


Figure 2 Log correlation between normalised (by a common constant) complexity measures and ant communication time. Kolmogorov complexity (by means of an Algorithmic Probability based CTM measure) and Logical Depth (also measured by BDM) display the greatest correlation, with longer times for more complex K and LD. Shannon Entropy and lossless compression (BZip2) display no sensitivity to differences in the sequence.

Fruitflies' behaviour in environments with little or no input stimuli is not random

In the *Drosophila* experiments (Maye et al., 2007), yaw torque binary (right or left directions) behavioural sequences for tethered flies in the virtual reality flight arena were recorded in three environments for up to 30 minutes, as described in our Methods section.

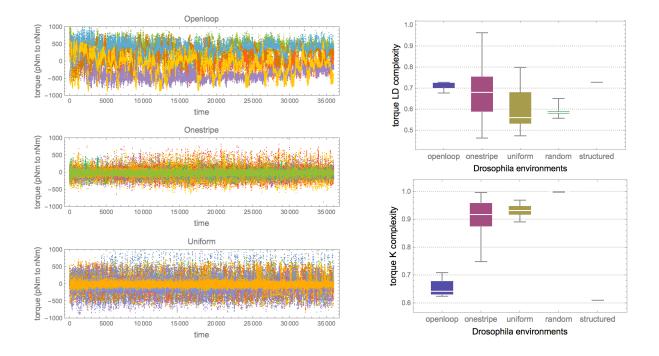


Figure 3 Left: Raw yaw torque series of the three fruit fly groups (about 38,000 data points from a 30 minute recorded flying period). Right top: Box plot of the series' Kolmogorov complexity as measured by CTM over all flies in the three groups (6, 18 and 13). Each replicate was given a different colour. Right top: In agreement with the results in Maye et al., (2007) the median complexity of the openloop group is the most removed from (algorithmic) randomness. The values were normalised by maximum K complexity according to CTM (as compared to the substrings of greatest complexity as calculated from CTM). Right bottom: Box plot of the series' Logical Depth complexity as measured by CTM over all flies in the three groups.

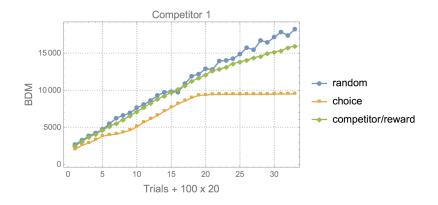
The results in Figure 3 suggest that the openloop group is the one with significant highest median structural complexity (Logical Depth), hence suggesting greater causal history or calculation and distance from randomness, while the other two groups are closer to pseudo-randomly generated sequences using a log uniform PNRG. This supports the original authors' findings but adds the fact that uniform stimuli seem to have a lower effect than no stimulus, and that no stimuli also leads to different behaviour, perhaps as a strategy to elicit environmental feedback. In both plots all values were normalised by maximum LD complexity to have them between 0 and 1. In both box plots the trivial sequences consist of 1s, and therefore are maximally removed from randomness for Kolmogorov complexity (but are closer to randomness in the LD plot). As shown in Figure 3, the series of fruit fly torque spikes for the three groups of fruit flies had different Kolmogorov complexities, with the openloop group being the furthest removed

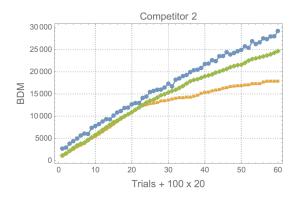
from algorithmic randomness and high in logical depth, suggesting an algorithmic source. This strengthens the authors' (Maye et al., 2007) conclusion that the same group was the most removed from normal randomness, and therefore that fly brains are more than just input/output systems, and furthermore that the uniform group was the closest to a characteristic Levy flight, which amounts to a falsification of the alternative hypothesis that in the absence of stimuli flies behave randomly, as their neurons would only fire erratically, displaying no pattern. Here, however, the results suggest that in the absence of stimuli the flies are even more challenged to find different flight strategies, perhaps seeking stimuli that would provide feedback as to their whereabouts. Moreover, as shown in Figure 3, by being able to measure the subtle differences in complexity along the various sequences, the variance provides another dimension for analysis---of the ways in which different flies reacted to the same environment.

Rats switching to random behaviour in environments of increasing complexity

To the experimental data of Tervo et al. (2014) (binary behavioural sequences representing L for Left and R for right depending on the choice of the animal and the prediction of a virtual competitor), we applied lossless compression, BDM and BDM LD. BDM and compression showed the expected complexity for each set environment (see Figures 6 and 7), with the first one (Competitor 1) displaying the lowest randomness for both the animal and the competitor/reward sequences (the competitor's behaviour is a Boolean function of the reward sequence given by (choice & reward) or (~choice & ~reward)). The reward sequence encodes whether or not the competitor predicted the animal's choice and therefore whether it was given a droplet---when avoiding the competitor's choice---or not. The goal of the rats was to outsmart the competitor's behaviour, but that does not necessarily mean an increase in a rat's behavioural Kolmogorov complexity (randomness), because it can fool the competitor with a simple strategy, as is the case for Competitors 1 and 2, and by switching to random-looking behaviour in the case of Competitor 3. This variation of animal complexity over time, going from high complexity to lower complexity, can be observed in Figures 6 and in Table 2 where a ranking is provided of learning capabilities per rat for every environment. In the environment with Competitor 1, a simple 3-tuple

behavioural strategy outsmarts the competitor's behaviour with a strategy of low complexity by keeping the frequency of R and L choices at about 0.5 but following very simple patterns that the competitor does not follow (the alternation of LLR and RRL or RLL and LRR). On the other hand, logical depth shows that the structural complexity of the animal always ends up matching the structural complexity of the competitor, and is never more or less than is required to outsmart it. From BDM and compression it is also clear that the 3rd environment is of lower structural complexity, which is consistent with the conclusion of the neural experiment that rats switched to stochastic behaviour when they were unable to outsmart the competitor, even when it appears that the mean is actually very similar when BDM and Compress are of lower complexity. This is not a surprise because the behaviour of the competitor is not algorithmically random; it only appears random to the rat, which in turn tries to behave randomly. But it does so not with greater complexity than the competitor but again only matching the complexity of the competitor, and because after all it is unlikely that the rat is really behaving in an algorithmically random fashion, but rather simulating random behaviour, the difference being that it is actually performing some computation tracking its immediate history so as not to repeat movements, given that probabilistically, statistical randomness would allow a long list of L or R, which is not optimal. Hence it has to go beyond probabilities and truly try to simulate algorithmic randomness, thus also increasing the required computation to reproduce the desired random-looking behaviour and therefore its logical depth.





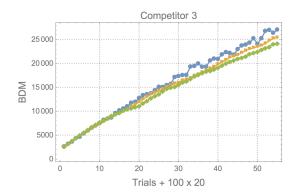
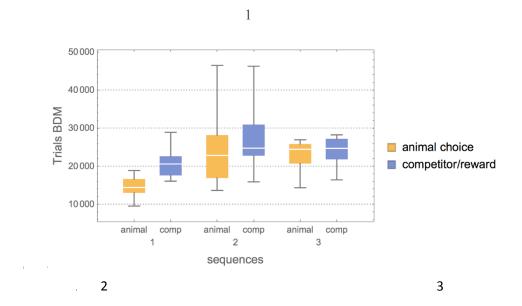


Figure 4 Top: The same rat number 6 in the three different environments with different virtual competitors. With Competitor 1 this particular rat shows two kinds of "phase transitions" leading to a decrease in its behavioural complexity.

In Figure 4, the common strategy appears to be to start off by displaying random behaviour to test the competitor's prediction capabilities, switching between different patterns up to a point where the rat settles on a successful strategy that allows it to simply repeat the same behaviour and yet receive the maximum reward after fooling the competitor. For Competitor 2 (Bottom left), this phase comes later, given that this new virtual competitor is slightly more sophisticated. For Competitor 3, the rat is unable to outsmart it because it implements a more sophisticated predictive algorithm and the rat either cannot settle on a single strategy and keeps performing a random search, or decides to switch to or remain in a particular mode after finding itself outsmarted by the virtual competitor.

As Figures 4 and 5 show, these results seem to suggest that the rats either switch to random behaviour on purpose, or continue in the random mode they started out in as a testing strategy to gauge the competitor's capabilities. However, as shown by the neural record experiments (Tervo et al., 2014), the rats eventually suspend brain activity, seemingly after finding that they cannot devise an effective strategy. But the results here build upon the previously reported conclusions that the rats seem to start with a high (random) complexity strategy in the very first trials before settling on a single specific strategy, if any. As shown in Figures 4 and 5, against Competitor 1 rats quickly settle on an optimal strategy of low complexity that keeps rewarding them, thanks to the poor predictive capabilities of the virtual competitor.

But as Figure 6 shows a representative case (and not a special one for Competitors 2 and 3), we see that animals make the transition later (Competitor 2) or never make it (Competitor 3). Plots in Figure 6 show the results of three algorithmic information-theoretic complexity measures applied to the behavioural sequences for both animals and competitors (comp) in all three environments of increasing complexity (more powerful virtual competitor predictive capabilities). One first observation is that the rat behaviour closely follows that of the competitor. For BDM and Compress (Fig. 6), the complexity against Competitor 1 of both the animal and the competitor behaviour are low but the gap between medians is large, meaning that the animal quickly outsmarted the competitor. Against Competitor 2 (for BDM and Compress), however, not only is an increase in Kolmogorov complexity but the median gap between the animal's behavioural complexity and the competitor's is smaller and the variance is greater, meaning that the animal seems to have explored more strategies of different complexity, and finally against Competitor 3 (same figure) the medians match at higher Kolmogorov complexity (random-looking behaviour).



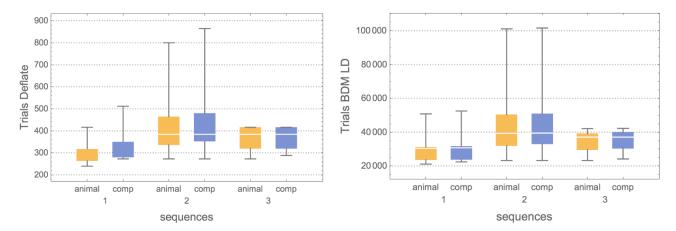


Figure 5 Top: Logical Depth (LD) estimations confirmed the nature of the strategy against Competitor 3, where there is a decrease in structural complexity as compared to the interaction with Competitor 2, hence suggesting that the animal remained in a stochastic mode of low Logical Depth but high Kolmogorov complexity (as shown by plots 1 and 2). An ANOVA test confirmed the mean differences among the 3 groups in each case.

The Spearman ranking tests among BDM and BDM LD in the three environments suggest, however, that intelligence can only be defined by task or environment in this experiment and for this set of animals, because no significant correlation was found in the ranking for different competitor experiments after a Kolmogorov-Smirnov (Table 2) test to determine the separation between animal and competitor behavioural complexity. In fact, there are 2 ways of outsmarting the virtual competitors that are confounded in the complexity curve: either the animal learns fast and maximises gain (keeps the competitor's behaviour complex), or minimises effort (reflected in the decrease in its own complexity). Hence the curves diverge.

Table 2 A Kolmogorov-Smirnov comparison of the animal's choice and the competitor's complexity curves may provide a ranking of intelligence in a given environment, with the smallest values where the curves are at the greatest remove from each other and therefore signifying the fastest the animal has potentially settled on a successful strategy. No significant correlation was found among the different environments, with some animals consistently coming out on top or at the bottom, suggesting that animals performed differently in different environments.

Animal number	Kolmogorov-Smirnov statistic
3	4.88022 x 10 ⁻⁶⁰
6	1.083 x 10 ⁻¹⁷

1.6514 x 10 ⁻¹²
1.3695 x 10 ⁻¹⁰
2.74921 x 10 ⁻¹⁰
7.5875 x 10 ⁻⁹
0.00045
0.001
0.003
0.012
0.223
0.55

Figure 5 shows how the structural complexity of the animal's behaviour matches that of the competitor, as suggested in Zenil et al., 2012b (this seems to indicate, however, that the match is with Logical Depth complexity and not Kolmogorov complexity). That Logical Depth, a measure of sophistication, is greater in the second experiment, means that indeed both the algorithm and the animal behaviour require more computational resources than in the 1st and 3rd experiments, where there is less consideration given to behavioural history, as the original paper reporting the neural experiment claims. This is also in agreement with what we found by applying both lossless compression and BDM.

It is also interesting to look at this asymptotic behaviour of both the animal and the competitor (see Figure 4), as it indicates a period of training before the rats start overtaking the competitor with an optimally rewarding strategy. Indeed, for the experiment with Competitor 1, the training period is very short; between 100 and 300 trials on average are needed before the curves start to diverge, indicating that the animal has outsmarted the competitor. In fact this can be advanced as a potential objective measure for animal intelligence, and one can see that subjects 3 and 6, for example, are among the fastest learners, the quickest at finding a good strategy, while subjects 11 and 12 are slow, a ranking based on a Kolmogorov-Smirnov test being provided in Table 2. Against Competitor 2 (see Figure 4 and Sup. Figure 2), again the rat has a training period where it matches the virtual competitor's behaviour before outsmarting it (the gap

indicates that there is a reward even in the face of lower animal complexity, which means it has cracked the competitor's behavioural code). Against Competitor 3 (see Figure 5), however, the animal is truly challenged and chooses to behave randomly, to which the learning algorithm reacts accordingly. Thus the two match in manifesting high Kolmogorov complexity as compared to the previous cases.

For Competitor 2, the Logical Depth increases because both the animal and the virtual competitor are engaged in a computation that requires slightly more computing power and time than when playing against Competitor 1. However, for Competitor 3, the Logical Depth decreases again, as an indication of either greater simplicity or randomness, which in this case is in agreement with the experiment. And taking into consideration the result with BDM, it is randomness that is introduced in the animal's choice of behaviour against Competitor 3, which is in full agreement with the results reported in the independent study (Tervo et al., 2014) and in the clinical experiments measuring cortical feedback to quantify brain activity during the performance of the tasks.

Conclusion

We introduced a common framework for cognitive behaviour testing. Having analysed the results of 3 previous landmark studies, we found we could reproduce and validate their results. Where the authors put forward intuitive conjectures, we were able to quantify and provide formal verification of their surmises, and where they were formal but were using diverse ad hoc tools, we provided a unifying platform. The tools introduced here contribute to modelling animal behaviour and to discovering fundamental mechanisms.

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Supplemental Material

Block Decomposition Method (BDM)

The Block Decomposition Method (Zenil et al. 2014) is used to approximate the algorithmic probability of longer sequences the calculation of which is computationally infeasible, given the number of Turing machines that it would be necessary to run in order to have a statistically significant frequency value. Unlike traditional lossless compression algorithms used to estimate K, the Block Decomposition Method (BDM) is capable of dealing with short sequences and has been successfully applied to human cognition (Gauvrit et al., 2014b and Kempe et al., 2015b) as well as to algebraic and topological characterisations of graph theory and complex networks (Zenil et al., 2014).

The method consists in decomposing a long sequence into shorter, optionally overlapping sub-sequences, the Kolmogorov complexity of which can be estimated by running a large set of random computer programs in order to estimate their algorithmic probability. For example, the sequence "123123456" can yield, with a 6-symbol window with a 3-symbol overlap, the two subsequences "123123" and "123456", i.e., what is known as *k-mers*, in this case 6-mers, all substrings of length 6. BDM then takes advantage of possible repetitions by applying the following formula:

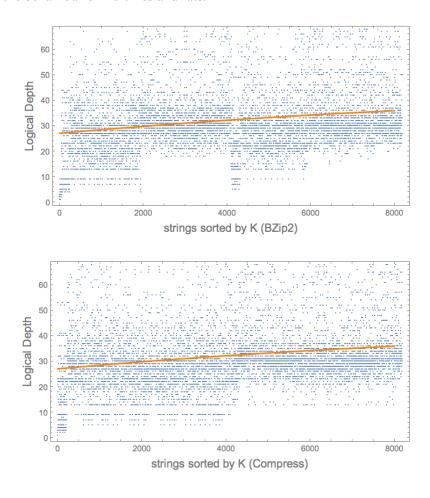
$$C(s) = \sum_{p} (log 2(n_p) + K(p)),$$

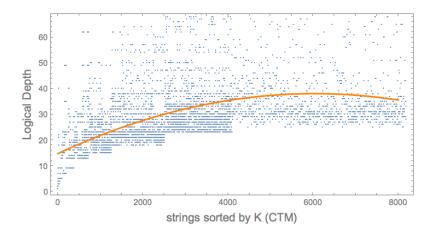
where the sum ranges over the different subsequences p, n_p is the number of occurrences of each p, and K(p) the complexity of p as approximated by CTM. As the formula shows, the Block decomposition method (BDM) takes into account both the local complexity of the subsequence and remote regularities by repetition of the same substring in the original sequence.

BDM is a divide-and-conquer algorithm that extends the power of the *algorithmic Coding Theorem*Method (CTM) that is computationally intractable (see Figure 1 and Supplemental Material).

Validation by numerical correlation of numerical estimations of K and LD

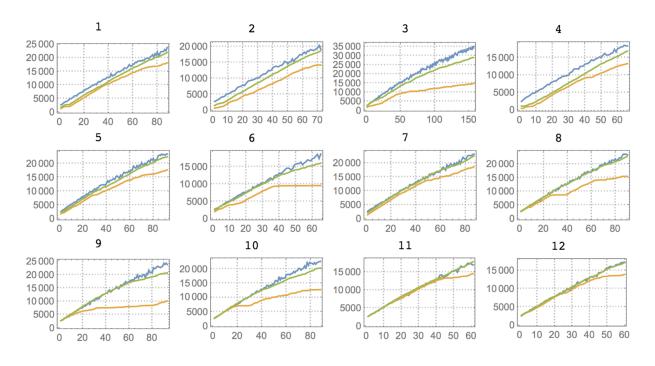
Comparing the results of LD by running a large set of enumerated standard Turing machines of increasing size, it becomes clear that approximating K by traditional lossless compression algorithms does not conform to the theoretical expectation of low LD for lowest and highest K values (see Figure 2), nor can they be usefully applied to short behavioural sequences (Delahaye and Zenil, 2011 and Soler-Toscano et al., 2014), such as the ones from a well-known behavioural experiment with ants (Table 1) and in more recent studies of the behaviour of fruitflies and rats.





Supplemental Figure 1 Scatterplots showing correlation between approximations to K and LD by means of lossless compression and CTM for all 2¹² bit strings up to length 12. Only CTM conforms to the theoretical expectation, that is, it displays lower LD values for low and high K values as shown in the fitting of a quadratic curve (bottom). Lossless compression, however (both Compress and BZip2 algorithms) displayed a trivial correlation with LD. The goodness of fit is less relevant than the trend that conforms to the theoretical expectation and yields a concave curve (bottom).

Supplemental figure 1 shows the results of running the CTM algorithm for numerical approximations to both LD and K in comparison to lossless compression algorithms. Applying a nonlinear least-squares regression (curve fitting) of Compression and CTM estimations to K against CTM estimations to LD using a quadratic function with best fit equation 14.76 + 0.0077x - 6.4X10⁻⁷x², it becomes clear that only CTM conforms with the expected theoretical result, where both Kolmogorov simple and Kolmogorov random strings are assigned lower Logical Depth. This is because random sequences, like trivial ones, are not the result of a sophisticated computation from their shortest descriptions. Indeed, if a sequence is random, then its shortest description is of about the same original length, and therefore the decompression instructions are very short or nonexistent. And if a sequence is trivially compressible, then the instructions for decompressing it may also be expected to be very simple. It is right in the middle that high sophistication or depth is to be found.



Supplemental Figure 2 Complexity (BDM) plots for all 12 individuals (rats) against Competitor 1. For Competitors 2 and 3, Figure 5 shows a representative case, while the rest of the plots are in the Supplemental Material. Colour legends and axis labels are the same as in Figure 4 (visible online only).

Further discussion

As shown in (Zenil et al., 2013b), if the environment is predictable, the cost of information processing is low, but this result also suggests that if the environment is not predictable, the cost of information processing quantified by logical depth is low if the stochastic behaviour strategy is adopted, hence providing an evolutionary advantage (Zenil et al., 2013b). This strengthens one of the studies (Tervo et al., 2014) conclusion that environmental complexity drives the organism's biological and cognitive complexity.

While the construction of an internal mental model that effectively discerns the workings of a competitor could generate a successful counterpredictive strategy, apparently random behaviour might be favoured in situations in which the prediction of one's actions by a competitor or predator has adverse consequences (Nash, 1950; Maynard Smith and Harper, 1988). Experiments we considered in this paper also relate to new developments in Integrated Information Theory, related to an approach to consciousness that

proceeds via a mathematical formulation (Tononi; 2008). Consciousness necessarily entails an internal experience, and here one indication of such an experience is the internal computation necessary to filter out or adopt non-random strategies in the absence of stimuli, and another is the way in which the apparent randomness of a rat's behaviour may actually result in the rat engaging in a sophisticated computation, even while ignoring sensorial input from the competitor or predator, as suggested in the neural recording experiments. Logical Depth is an indication of a causal history that requires more than simple feedforward calculations connecting sensors to actions. Some other connections between integrated information and algorithmic complexity are in Gauvrit et al. (in press).

The approach introduced here based on measures of algorithmic complexity may help to interpret data with tools complementary to the classical ones drawn from traditional statistics. For an animal to exploit the environmental deviation from equilibrium, animals must go beyond probabilities, i.e., beyond merely calculating the frequency of moves and beyond trivial entanglement with the environment. Animals clearly distinguish between environments of different complexity, reacting accordingly. In (Zenil et al., 2012b) it was shown how animals would need to cope with environments of different complexity in order to survive and how this would require --- and may explain --- the evolution of information storage and the process of learning. The results here reported point out towards this direction. The approach may also find applications in designing cognitive strategies and measures in robotics and artificial intelligence based on complexity-based strategies and adaptation (e.g. Zenil, in press).