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The Indirect Verification of Minimal Two-generator Model of Homeostatic Drinking by Complexity Examination

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In the course of previous examinations, it has been suggested that minimally two lick pattern generators have to take part in the formation of temporal patterns of homeostatic drinking. The drinking pattern of five rats was investigated, subsequently analysed and compared to simulated data. As the interaction of the two generators changes by the progress of satiation, the dynamics of drinking have to change too. In this experiment we demonstrated this nonlinear dynamical change by the examination of algorithmic complexity which reflects the nature of motivational changes and that the proportion of the change of complexity is in harmony with our model of homeostatic drinking.

1. Introduction

The rhythmical, stereotyped licking behavior of mammals during drinking is analogous with the stereotyped series of movements formed by certain generators—Central Pattern Generators (CPG)—which have been observed and described in invertebrates. While the analysis and modelling of the CPG in invertebrates has taken place in detail (Selverston, 1980; Beer & Chiel, 1995; Calabrese, 1995; Dean & Cruse, 1995; Harris-Warrick *et al*., 1995; Hooper, 1995), we know very little about the nature of CPG forming the licking and drinking behavior in mammals, though some work has analysed the input side of drinking CPG (DCPG) in detail. It has been proved that licking is a pre-programmed ballistic movement where the effect of the tactile stimulus will appear late in the licking pattern (Mamedov & Bures, 1984). Not only tactile but gustatory stimuli also influence the working of DCPG. Different concentrations of sugar solutions shape different drinking patterns, changing the frequency and variance of the intervals appearing in the drinking–licking records (Davis & Smith, 1992).

Analysis of the temporal pattern of homeostatic drinking behavior may reveal the nature of the control exerted by the DCPG on the output pattern. As drinking was organized into typical temporal patterns—bouts—during most of the experiments, we have already examined the intra-bout and inter-bout intervals and measured changes of the bout lengths along a satiation process (Karadi & Bende, 1995). Three temporal measures during satiation showed three different pictures, divergent from each other. Therefore we assume that at least two generators must be involved in the formation of a licking pattern. The CPG network character in invertebrates and how many generators contribute to the formation of the behavior have been explored in much detail. Up to now, only one research paper examined which part of the brain is responsible for the drinking–licking patterned behavior of rats: e.g. Wiesenfeld & Halpern (1977) showed that during licking a slow wave oscillation could be detected in the nucleus hypoglossus. The number of generators and functional relations between them have not yet been verified. To obtain more confirmation for the minimal two-generator model, we examined the output side of

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DCPG. Previously (Karadi & Bende, 1995), we took the temporal pattern of drinking apart and examined various different lick patterns. Otherwise, the patterned drinking can be treated as a complete series of events and can be analysed as a dynamical behavior of a system as a whole. This way, we can examine what kind of dynamical changes happen to the system through the restoration of homeostatic deficit and we can conclude how many generators, and in what proportion of them, do take place in the formation of these dynamics, because other statistical analyses of drinking patterns (distribution test of inter-lick intervals, log-survival analysis) are unable to confirm well the number of generators in the record. The customary time series methods used for dynamical systems analysis (Lyapunov exponentials, correlation dimension calculation) are difficult to use for some biological phenomena due to the few numbers of recordable data, so we applied algorithmic complexity examination which is used for the dynamical analysis of smaller data pools.

2. Subjects and Data Acquisition

The experimental subjects were adult Wistar rats from both sexes ($N = 5$), weights 300–350 g). The animals were housed individually in their home cages under 12-hr light/dark cycles, where they could eat and drink ad lib standard rat food and tap water except on test days. Before testing, a 24-hr water deprivation was introduced, and the drinking tests were running for 3 days in 1-hr daily sessions. During the experimental sessions Ss. could drink tap water ad lib from a spout. We moved the animals from their home cages and put them into the test cages, where they drank water from the spout. Across a drinking recess, we measured the time between tongue-movements (inter-lick intervals) with photocell lickometer. Photocell signals were fed into a computer and recorded by software developed by ourselves. Data consisted of durations of licks, inter-lick intervals and of lick frequencies. The total recording period was divided into six 10-min timebins, to record and to analyse subsets (trend) of data.

The mean amount of consumed water during experimental sessions (Fig. 2) showed a typical satiation curve, in as much as rats consumed nearly 50% of the total 1-hr intake within the first 10-min period, and the trend became asymptotic as satiation progressed. During the analysis, derived data records, e.g. lick-bouts and else, were worked out, however, the complexity measures, applied below, used only inter-lick interval lengths for computation. Analysis of differences of bouts themselves, etc. were not analysed here.

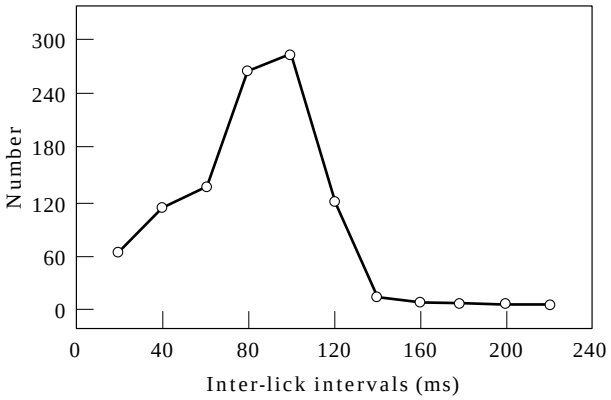

FIG. 1. Distribution of the averaged inter-licks intervals of five rats during a 1-hr session (intervals longer than 240 ms omitted due to their few numbers).

3. Complexity and its Measures

Time series formed by biological systems as a consequence of the changes of the inner environment, often show a wild scale of dynamical behavior. Dynamics may change between chaotic, irregular, highly complex and the regular and less complex behaviors. Lyapunov exponentials characterize time series mainly qualitatively (express the presence of chaos in it), while the correlation dimension describes the system quantitively (measures its complexity; Wolf *et al*., 1985; Kaplan *et al*., 1991). The chaos theory gives two methods of examination for the characterization of a dynamical system. The disadvantage of these methods is the great number of data points for reliable calculation (their demand for acurate calculation is 10 000 points), so these methods cannot be used for the dynamical changes shown in the biological system during the formation of satiation during drinking, as we can get only maximally 4000 data points from an animal during a 1-hr testing. That is why we chose the less data-demanding algorithmic complexity examination for the analysis of the temporal pattern of drinking behavior. Before we detail the examination, we have to define the meaning of complexity. In terms of chaos theory, the complexity of a dynamical system is equal to its dimension. Dimension is the number of those dynamical variables that take part in the formation of the given signal. The dimension of a regular periodical signal is 1, while the level of a random sequence may be practically infinite. Another definition of complexity, similar to this one, is used for measuring algorithmic complexity. According to Chaitin (1975),

the complexity of a signal is equal to the minimal length of algorhythm with which we can generate the given symbol sequence. Papentin (1980) modified this definition: complexity of a sequence is equal to the length of the minimal algorhythm with which we can describe a sequence. Hinegardner & Engelberg (1983) simplified further: ". . . complexity to be the size of the minimum description of an object". To our view, definition of complexity means the minimal algorithmic length that is equal to the number of those dynamical variables that characterize the given system. According to Rapp's algorithmic method (1994), a given complexity measure gives a reliable value if we look at the *median* of the original time series and we encode the given biosignal to *binary series* according to this. In the case of drinking behavior the median of the inter-lick intervals (ILI) was calculated. We assigned the 1-hr drinking time into six 10-min bins and thus we got six pieces of the record. In these pieces (timebins), the intervals longer than the median got a value of 1, those less than or equal to it got 0. We measured the complexity of the binary sequence by the method detailed below. As follows, by Rapp (1994) and his colleagues' instruction for measuring of complexity, the procedure is best described by considering an arteficial example. There is a given binary sequence:

$$S_1 = 0\ 1\ 1\ 0\ 1\ 0\ 0\ 1\ 1\ 0\ 1\ 0\ 0\ 1\ 0\ 0$$

First we look for repeated pairs of symbols and we sign them with different symbols.

$$a = 0\ 1$$

The pair 01 is repeated five times and we substitute this pair with a new symbol "*a*". The sequence then reduces to

$$S_2 = a\ 1\ a\ 0\ a\ 1\ a\ 0\ a\ 0\ 0$$

The searching of repeated pairs is continued. The pair *a*0 is repeated three times. The symbol "*b*" signs this pair.

$$b = a0$$

$$S_3 = a\ 1\ b\ a\ 1\ b\ b\ 0$$

According to Rapp, the compression of a given sequence can occur only if a pair is repeated at least three times. In S_3 we cannot find symbol pairs which are repeated more than twice. Therefore we begin the search for repeated triplets. Now, triplets disappear too.

$$c = a\ 1\ b$$

The $a\ 1\ b$ triplets are compressed in "*c*" symbol,

$$S_4 = c\ c\ b\ 0$$

$$S_5 = c^2\ b\ 0$$

In S_4 the repeated symbol (*cc*) is expressed as exponential (c^2) in S_5.

Further we cannot find repeated sequences. So we encoded the original signal to a minimal sequence, and arrived at a quantitative definition of complexity.

"The grammar complexity of the original message is defined to be the sum of the complexities of each component in the compressed message (Rapp, 1993)." In S_5 we can find three symbols ($c\ b\ 0$), coding the binary sequence, and these symbols contribute 1 to the sum: "*a*" and "*b*" symbol take a part with 2 because they contain two symbols (repeated pairs): "*c*" with 3 because it contains three symbols and "c^2" takes one occurence of exponents 2 and it contributes $\log_2 2$ part to the sum:

$$\text{Complexity} = [3 + 2 + 2 + 3 + \log_2 2] = 11$$

The square brackets indicate that the integer part is to be taken.

Since the lengths of sequences were not equal in the six 10-min bins, we calculated relative complexity:

$$\text{Relative Complexity} = \text{Complexity/Length of Sequence}$$

So the complexity values in each bin become comparable and we can follow how the dynamics of drinking change within the 1-hr drinking session.

4. Results

Before the presentation of complexity scores we demonstrate the averaged cumulative intake curve as percents of the total intake (Fig. 2), as well as the distribution of inter-lick intervals during the 1-hr drinking sessions (Fig. 1). The intake curve shows the pure satiation effect of the water drinking.

In the case of all rats the 3-day, 1-hr drinking sessions were processed in 10-min decompositions and thus we got six complexity values for 1 day. In the first step we averaged the 3-days' values of each rat. One-way ANOVA analysis was used to check that none of the daily complexity values differed significantly from the others in the case of each animals. The ANOVA results in the case of each animal: 1st rat ($n = 18$; df: 2,15; $F = 0.008$; $p = 0.99$; n.s.); 2nd rat ($n = 18$; df: 2,15; $F = 0.189$; $p = 0.82$; n.s.); 3rd rat ($n = 18$; df: 2,15; $F = 0.866$; $p = 0.44$; n.s.); 4th rat ($n = 18$; df: 2,15; $F = 1.55$; $p = 0.25$; n.s.); 5th rat ($n = 18$); df: 2,15; $F = 1.3838$; $p = 0.19$;

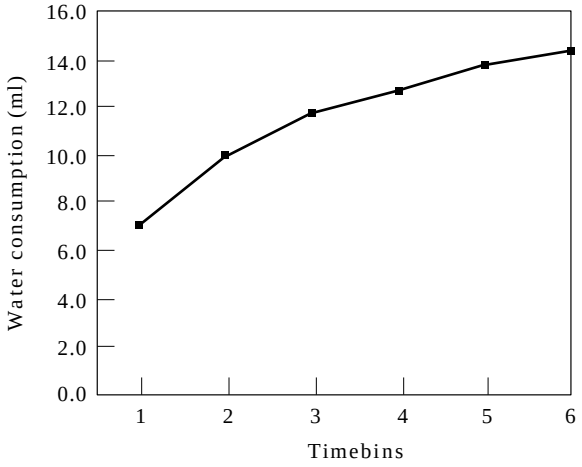

FIG. 2. Averaged cumulative intake curve of five rats during a 1-hr drinking sessions.

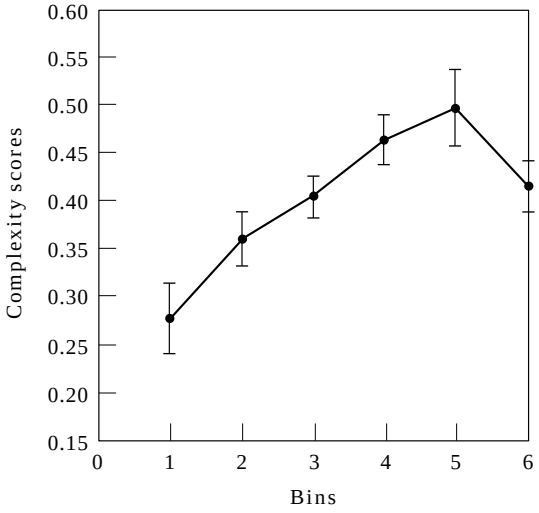

FIG. 3. Change of the relative mean complexity (±SEM) scores during real drinking. *x*-axis represents the 10-min bins of 1-hr sessions and *y*-axis depicts the complexity scores.

n.s.). There were no significant differences between the 3-day complexity values in the case of each rat. We also used one-way ANOVA checking that there were no significant differences between the rats' values ($n = 30$; df: 4,25; $F = 1.851$; $p = 0.15$; n.s.). The animals' complexity values therefore could be considered as homogenous. After that we also averaged the complexity values of five rats, yielding five-rat averaged relative complexity values in 10-min decompositions (timebins) (Table 1).

Figure 3 shows the averaged relative complexity changes in the 1-hr session. We see that the complexity rises continually until the fifth 10-min bin, then in the 6th 10-min it falls to the value measured in the 3rd interval.

5. Discussion

Up to now, none of the earlier studies addressed directly the dynamics of drinking behavior by the method of complexity analysis.

According to our viewpoint, complexity analysis presents new information about this behavior. The usage of this analysis demonstrated that we can reveal the pure nonlinear dynamics of this behavioral (drinking) system. Standard methods (Lyapunov, correlation dimension) cannot explore fine dynamical changes in small data sets through the great error level of the measure in such cases. It has not been decided whether two or three generators take place in formation of behavior of time series, based on consummatory behavioral models (Sibly *et al*., 1990; Berdoy, 1993). We have found, that in the shaping of drinking pattern, two generators, one Bout and another Non-Bout generator take place (results: Karadi & Bende, 1995). Our complexity examination supports the validity of this minimal two-generator model. The animals were made thirsty for 24-hr, consequently they were drinking without long breaks in the first 10 min of the session: they produced long bouts with little stops for inter-bout intervals. The variability of intra-bout intervals is very little, as our earlier research showed. As the intra-bout intervals dominate in the first time series in the first bin, their complexity is small. From the beginning of the 2nd 10-min, we see the teamwork of the Bout and Non-Bout generators. As the variability of the inter-bout intervals proved significant and number and lengths of intervals increase in the drinking pattern as satiation proceeds, that is why the complexity of the pattern increases continually. This can be seen until the fifth 10-min bin and in the 5th bin the value of complexity is the greatest. It is interesting that complexity does not grow further, but in the last 10-min it falls back to a medium level. This can be explained best by the fact that animals often

TABLE 1
Averaged relative complexity scores of the five rats in the six 10*-min bins of the* 1*-hr drinking session*

Bins	Means ± SE
1	0.278 ± 0.035
2	0.36 ± 0.027
3	0.404 ± 0.020
4	0.464 ± 0.025
5	0.496 ± 0.038
6	0.414 ± 0.026

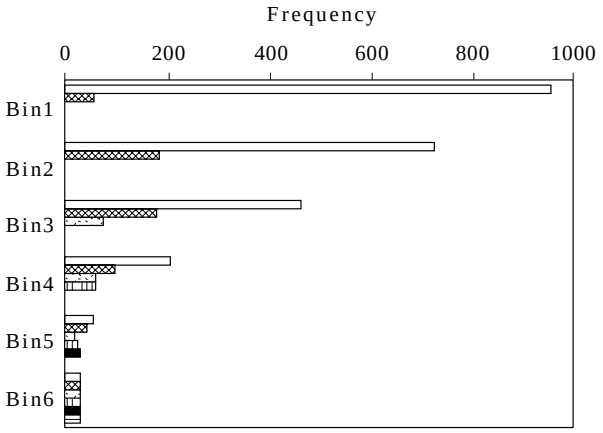

FIG. 4. Histogram showing the frequency distribution of inter-lick intervals in six different timebins during 1-hr simulated drinking sessions. Total number of intervals per bin is decreasing continuously from 1st to 6th. The proportion of the number of the "bout-" (short) and of "non-bout" (longer) intervals are decreasing regularly so that the decreasing number of "intra-bout" intervals has been progressively divided by the increasing number of "non-bout" intervals. The lengths of "intra-bout" intervals were set uniformly to 0.020 s in all bins, while those of "non-bouts" were chosen randomly from progressively longer time intervals (from 0.02 to 1 s in the first two bins, and then from intervals ranging from 1 to 2, from 2 to 3, from 3 to 4, then from 4 to 5 s consecutively in the further bins, see Table 2.) Values of each inter-lick lengths were chosen randomly from a uniform random number distribution of the above ranges. Satiation by the data increases continually during the simulated session, and the number of licks gradually reaches zero. *y*-axis assigns the bins and *x*-axis represents the number of intervals. □ 0–2, ⬚ 2–100, ▩ 100–200, ▥ 200–300, ■ 300–400, ▤ 400–500.

restart drinking in the last minutes of a lengthy test, therefore, if at least two generators are involved, the Bout generator starts to dominate again. Thus in he

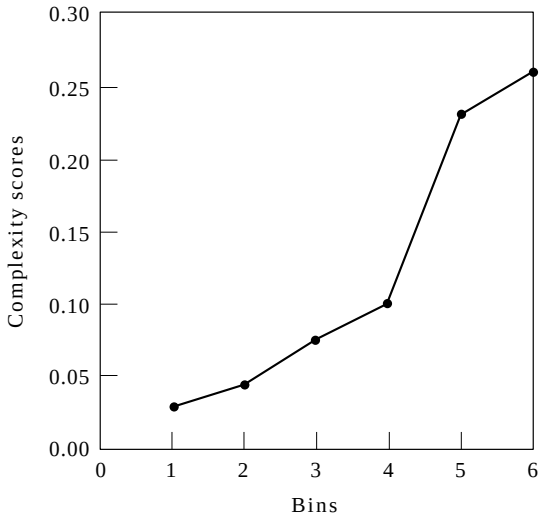

FIG. 5. Change of the relative complexity scores during simulated drinking. *x*-axis represents the 10-min bins of 1-hr simulated session and *y*-axis assigns the complexity scores.

TABLE 2

Numbers of the simulated inter-lick intervals, representing a regular slowing rate of homeostatic drinking of an "ideal rat"

Interval range (ms)	Bin 1	Bin 2	Bin 3	Bin 4	Bin 5	Bin 6
< = 20	950	720	457	201	49	17
20–1000	50	180	173	94	40	16
1000–2000	0	0	70	52	15	13
2000–3000	0	0	0	53	20	12
3000–4000	0	0	0	0	26	18
4000–5000	0	0	0	0	0	24
N:	1000	900	700	400	150	100

As it is shown, the first two timebins contain only intervals shorter than 1 s. Explanation on Fig. 4

time series, the less variable intra-bout intervals take part with more impact, so the complexity of drinking decreases in the 6th 10-min period. Explanation with *one* simple frequency generator could hardly lead to the demonstrated results.

Figures 4 and 5 and Table 2 show interval frequency histogram and complexity values of an ideal, simulated rat drinking.

Simulated data were generated so that the satiation would increase continually (as is expected) and the proportion of longer inter-lick intervals, presumably, increase progressively. So by the increase of satiation the animal produces less and less bouts and has more, and longer, breaks between them. The complexity examination of this model shows that the complexity is increasing continuously, it is the greatest in the 6th 10-min and it does not fall back to a medium value. In the case of the real animal, the drop in the 6th 10-min may seem to be strange as the general opinion is that the 1-hr drinking completely restores the water deficit. The animal should not produce a thirsty drinking pattern formed on a medium satiation level in the last part. According to us the drinking in the last minutes is not necessarily homeostatic, rather perhaps it is similar to some adjunctive behaviors, like vacuum activity (Falk, 1977; Roper, 1983). To argue for or against this needs further research and data.

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