At the level of language, Drosophila's sex life is as rich as ours

Ruedi Stoop, Patrick Nüesch, Ralph Lukas Stoop, [†] and Leonid Bunimovich [‡]

†Institute of Neuroinformatics, University of Zurich and ETH Zurich
Winterthurerstr. 190, 8057 Zurich
‡Georgia Institute of Technology, Atlanta, Georgia 30332

Email: ruedi@ini.phys.ethz.ch

Abstract—Precopulatory courtship is a high-cost non-well understood mystery in animal world. Drosophila's (=D.'s) courtship shows marked structural similarities with its mammalian counterpart, suggesting its study to dissect origins, purpose and modalities of the phenomenon. From courtship videos, using a mathematical symbolic dynamics approach, we show that D.'s body language allows to express in addition to a coarse-grained population group membership also finer, individual information. From a formal language point of view, D.'s body language is shown to have a complexity of language that is equal or even exceeds that of human language.

1. Introduction

In animal world, courtship varies from simple rituals to complex communication-like behaviors. Despite its high costs, the origins and purpose of courtship are still not well understood. A probable hypothesis is that courtship is an evolutionary optimization mechanism that a species may or may not take advantage of in order to optimize its gene pool. Living in a simple and evolutionary fast environment, D. provides a well-suited testing case. Until recently, investigations were hampered by a lack of conceptual frameworks able to address these question. Behavior is characterized by rituals consisting of well-chosen sequences of individual actions. Since it is in the nature of these rituals that they need to be repeated if required, behavior has been characterized by sequences of indecomposable closed obits of indecomposable individual actions, so-called irreducible orbits of irreducible acts [1-2]. This is motivated by a successful nonlinear dynamics approach to chaotic systems, where it has been shown that complex systems can systematically be reduced to a minimal set of closed sequences of symbols (there called irreducible closed orbits), from where the system can systematically be approximated by taking ever more combinations of these sequences, starting with the shortest ones (for references see [2]). Using this encoding, it has been shown [1-2] that the body language of D. allows not only for the coarse-grained identification of an animal as a member of a particular population group (e.g., virgin, mature, mated female, normal vs. mutant fruitless male). The body language of D. is, moreover, driven by the clear purpose to convey individual information up to the limits permitted by the population group coarse graining property. Here, we do not pursue this aspect any further, but focus on the properties and in particular the power of the body language D. uses.

Over the centuries, the evolution of human language has been the subject of controversial discussions among philosophers, linguists and biologists. Yet, a consensus on what causes language to evolve and what are the effect of this on society has not been gained. Traditionally, language was thought of as a strictly culturally transmitted phenomenon, with little or no biological ties at all. In the second half of the 20th century, under Chomsky's influence who considered that language is located in the brain and therefore is subject to biological conditions [3-4], this view started to change. A fierce dispute raised on what the driving forces of the evolution of language could be. An important observation is that language - as any complex ability of humans or animals - is the result of natural selection [5]. Chomsky and scholars remained, however, skeptical about approaches seeing natural selection as the only direct origin. They suggested that language grammar may have emerged as a side-effect of the reorganization of the brain due to its growing size during the evolution towards the modern homo sapiens [6] (see also [7]). In order to study the evolution of language and to determine its driving forces, a classification of languages accounting for the changes undergone would be helpful. To capture the grammatical complexity aspect of languages, Chomsky and Schützenberger [8] proposed a hierarchical classification scheme, comprising grammars of increasing grammatical complexities: type t-3 (finite state; right / left regular) ⊂ type t-2 (context free) ⊂ type t-1 (context sensitive) ⊂ type t-0 (Turing machine). This classification has proven extremely useful in different fields of comparative sciences. It has been used to compare spoken human languages, to distinguish compiler languages, in the context of the theory of automata, and for classifying dynamical systems. On this background, the question naturally arises: Are more advanced organization forms generally equipped with more complex language structures? In our study, we will focus on a more specific - but similarly central - question: Do more complex organizations (society, intelligence,..) require language representations of increased grammatical complexity?

To answer this question, we compare the grammatical complexity of human language (which is known to fall mostly into Chomsky hierarchy type t-2 [8-9]) with experimental data from the precopulatory courtship body language of the fruit fly Drosophila [1]. To the best of our knowledge we use here for the first time Chomsky's classification scheme to characterize courtship and animal body language. Although the question by what Chomsky-type given experimental data were generated is in its narrower sense undecidable [11], we are able to provide the answer in a statistical sense: Namely, we show that it is very unlikely that the body language of the fly is generated by grammars of grammatical complexity lower than those of the human languages. For some cases, we even find indications that a type t-1 grammar underlies the generation of the observed sequences of fruit flies actions, which would even reach beyond the grammatical complexity of human language.

2. Experimental data

The data used in this study originates from experiments with the fruit fly Drosophila, where the courtship behavior of a pair of single fruit flies in an observation chamber is recorded and encoded in symbolic language [1-2]. For the behavioral study, a pair of flies is transferred into a chamber at fixed environmental conditions of 25 °C and 75% humidity. A camera with a high time resolution of 30 frames per second is needed to separate courtship behavior into the fundamental acts. Besides pairing single normal females in the immature, mature and mated states with single normal males, additionally fruitless mutant males [1] were paired with either mature females or with mature normal males, leading to five types of experiments. Since either of the protagonists gives rise to a time series, we obtain in this way ten classes of experimental time series.

Fundamental acts are body movements that can be freely combined with other fundamental acts. Tagging each fundamental act by an integer number, each camera episode is represented by a string or time series of these symbols. A mature female as the protagonist in the presence of a normal male, e.g., generates in this way a time series as

$$\omega = \{9, 17, 21, 20, 17, 20, 6, 21, 6, 21, 17, 18, 21, 25, 20,$$
$$17, 20, 21, 17, 18, 21, 17, 20, 9, 17, 20, 21, 20, 21,$$
$$17, 21, 17, 18, 21, 17, 21, 20, 24, 17, 18, 20, 21, 17,$$
$$21, 20, 17\}.$$

It has been shown in [1-2] that it is very likely that during D.'s precopulatory courtship, individual information is transmitted to the prospective partner. I.e., a real communication with essential information transmitted is relayed between the partners, which sheds a new light on the purpose of courtship. In the present report, we will, however, not focus on this aspect but address the grammatical complexity that underlies the generation of the courtship data.

3. Statistical generative grammar model

We start with the simplest grammatical model for the putative generation of the experimental time series. The lowest complexity (type t-3) grammar of the Chomsky hierarchy is equivalent to a random walk on the given set of symbols with probabilities given by the symbol frequencies observed in the respective experiments, but with no further restrictions imposed. Thus, if D.'s body language is of low complexity, it would be likely that observed strings fit well into the random walk model. From simulating the random walk model based on the observed symbol probabilities of each experiment, we obtained from each experimental file a set of surrogate files to compare with (throughout our investigations, we use $N_{sim} = 100$ simulated random walks). For the comparison, a figure of merit is used. Every time series $\omega = \{x_0, x_1, ..., x_L\}$ is characterized by products along the string of the probabilities $P_{in}(x)$ - measuring that a random walk starting at x_0 ends at point x - with $P_{out}(x)$ measuring the probability that a random walk starting at x reaches point x_L.

For the unrestricted random walk, these probabilities have the following form:

$$P_{in}(x) = \frac{n!}{n_1! \cdot ... \cdot n_{n_{symb}}!} \cdot p_1^{n_1} \cdot ... \cdot p_n^{n_{n_{symb}}},$$

$$P_{out}(x) = \frac{(N - n)! \cdot p_1^{(N_1 - n_1)} \cdot ... \cdot p_n^{(N_{n_{symb}} - n_{n_{symb}})}}{(N_1 - n_1)! \cdot ... \cdot (N_{n_{symb}})!},$$

where n is the number of steps needed to reach point x, producing n_j repetitions of the symbol tagged with index j.

The entropy H associated with a particular realization of string is based on the local walk-through probability $P_{through} := P_{in} \cdot P_{out}$, evaluated along the string, as

$$H_{through}(\omega) = -\frac{\log(P_{through}(\omega))}{L}$$

$$:= -\frac{1}{L} \sum_{i=1}^{L} \log(P_{through}(x_i))$$

$$=: \frac{1}{L} \sum_{i=1}^{L} H_{through}(x_i),$$

with $x_i = (n_1^i, n_2^i, ..., n_{n_{symb}}^i)$ the coordinate of point $x_i \in \omega$ in the symbol space.

Across the whole data set, we evaluated $H_{through}(\omega)$ for each experiment and the mean value of $N_{sim} = 100$ surrogate random walks for the underlying approximation process. Whereas the t-3 random walk model generates strings with similar $H_{through}(x)$ characteristics for approximately one third of the experimental data, for the remaining two thirds, this description fails. In the latter examples, the experimental $H_{through}(x)$ may dramatically differ from those obtained for the t-3 model: Clear peaks easy to identify in experimental $H_{through}(x)$ around finite positions x are very unlikely to be reproduced by a purely stochastic model.

Clear maxima leading to a pyramid-like shape of $H_{through}$ suggest that a change in the alphabet has occurred in the data.

To proceed further with those experiments that do not fit in the random walk model, we split the strings at the point of maximum $H_{through}(x)$, and model each partial string $\omega_{i,1}$ and $\omega_{i,2}$ separately as random walks. The resulting model is called a 'partial random walk' with (at least) $k = 2$ partial random walks. We first introduce (and justify the use of) a grammar able to generate $k = 2$ partial walks. In a second step, we describe grammars that enable multiple splitting of a string, leading to $k > 2$ partial walks. The $k = 2$ partial walk grammar generating strings $\omega = \omega_1\omega_2$ can be shown to be now of type t-2 (i.e. context-free), since a word $\omega = a^n b^n$, $n \in \mathbb{N}$ cannot be created by a type t-3 grammar. By modeling each of the two partial string independently with corresponding alphabet and frequency vector, the experimentally observed $H_{through}(\omega)$ from five experiments are much more likely to occur than with the previous model . The partial random walk model underlying type t-2 grammar can, however, only reproduce the characteristics of some experiments. The model remains to be inappropriate for about half of the data. To simulate the remaining experiments, the obvious solution is to expand the partial random walk model to more than $k = 2$ partial walks, using the following iterative approach ('t-3, t-2, t-1 model'):

1. Calculate $H_{through}(\omega)$ of each experiment ω. Simulate N_{sim} random walks of $k = 1$ and calculate the mean and standard deviation. If $|H_{through}(\omega) - \mu| < \sigma$: Stop, because the simple random walk describes ω well (the used distance measure could be refined to better weight the distance at step i of the walk, but our approach suits the purpose).

2. If $|H_{through}(\omega) - \mu| > \sigma$: ω does not fit the random walk model. Increase $k \to k+1$ by splitting the string at the point of max $H_{through}(x)$) resulting in $\omega = \omega_1\omega_2$.

3. For each partial string ω_1, ω_2 continue with point 1.

4. Results

This grammar generates partial random walks with $k > 2$ partial strings and can be shown to be indicative of type t-1 grammar. If we compare $H_{through}$ of the new grammar, we see that, finally, this grammar accounts for the experimentally observed strings.

The classification of D.'s body language provides a new insight into the behavior of the protagonists involved. As an example, the comparison between the behavior of all observed female flies and all observed normal males uncovers an interesting property: Whereas female flies tend to use type t-3 or t-2 grammars, normal males clearly lean towards type t-1.

A natural question is whether the obtained results could not in a simpler way be generated by a successions of type t-3 grammars. In order to investigate this possibility, we checked the occurrence of irreducible (i.e.: non-decomposable) closed orbits. Irreducible closed orbits provide not only the building blocks of dynamical systems [2], they also have been suggested to provide the mathematical basis for capturing what is normally in diffuse terms called 'behavior' [1]. For data generated by a succession of type t-3 grammars, their number should not differ in an essential way from the number obtained by simple type t-3 surrogates. We observed, however, a massive increase of the irreducible closed orbits from files that we classified as type-2- or type-1-generated. These results corroborate the - at that time somewhat speculative - expectation put forward in Ref. [2] that an increase of the number of closed orbits could serve as the hallmark of a higher grammar. Our - again: statistical - argument now pinpoints this view and justifies a conjecture that the underlying grammar is beyond type t-3.

5. Interpretation and conclusion

The high numbers of closed orbits found in the experimental data points to vastly recurrent structures, indicating that recurrent structures are implemented, but might not always be activated. Using the grammatical hierarchy proposed by Chomsky and Schützenberger as the classification scheme, D.'s precopulatory body language is not likely the result of the simplest grammar type t-3 (i.e., a random walk on a finite state automaton). It has earlier been found (and there is general agreement on) that natural human languages fall into the type t-2 of Chomsky's characterization (with among the European languages the Swiss-German and to a lesser extent the Dutch showing the highest degrees of grammatical complexity [7-8]). On the basis of our analysis one can safely say that D.'s body language is of no lesser grammatical complexity than the spoken language of humans. From our findings we also conclude that grammatical language complexity fails to cover essential aspects of language. In particular it is not possible to conclude from the language to the developmental level / intelligence of an organism. More complex worlds seem to not require more complex grammars. Moreover, the Turing machine is not as important as one could have believed. These findings are similar to the results from measures of complexity of prediction [13] and of computation [14], where, e.g., the highest measures of computation are usually triggered by the most trivial arithmetic operations, stripping these measures entirely from any 'content' or 'meaning'. Similarly, this is reflected in the most fundamental computational frameworks, the elementary cellular automata, where the biologically most interesting rules (able to embody long memory effects at the edge of chaos) do not include the Universal Turing rule 110 [15] (see [16]).

It may well be that the evolutionary anatomical changes

(the growing brain) have led to an outsourcing of loops and stacks to other areas of the brain, leading to a notion of awareness of these loops. During evolution, based on the usefulness of this concept (exploited in navigation or even more so in counting processes), these units may have enforced, enhancing the awareness and the purposeful use of these structures further. This in distinction to the animals that also possess these structures, but are not aware of them and do not use them purposefully. In the fascination evoked by the children's rhyme "Once there was a man with a hollow tooth and in this tooth there was a little box and in this box there was a piece of paper, on which was written: Once, there was a man.." we see a manifestation of this human ability. We suppose that no animal would find such a construct as fascinating as we do. Finally, let us mention that already Hofstadter's Pulitzer-winning bestseller "Gödel, Escher, Bach" [17] focused on this fascinating phenomenon.

Thus, the supremacy of human intellect cannot be founded on the formal grammatical complexity of the language being used. It rather emerges that also animals have recursive elements (these are often used for making the distinction between t-3 and t-2, see the in-depth discussion provided in [18]). It may, however, well be that only humans have a kind of awareness of recursions. From the present study we cannot distinguish whether the language has been learned or is programmed genetically, since this difference is not related to the complexity of the language, but we lean towards the genetical or towards a mixed mechanism.

References

[1] Stoop, R. & Arthur, B. "Periodic orbit analysis demonstrates genetic constraints, variability and switching in Drosophila courtship behavior", Chaos **18**, 023123 (2008).

[2] Stoop, R. & Joller, J. "Mesocopic comparison of complex networks based on periodic orbits", Chaos **21**, 016112 (2011).

[3] Chomsky, N. "Three models for the description of language", IRE Transcriptions on Information Theory **2**, 113-124 (1956).

[4] Chomsky, N. "Knowledge of language: its nature, origin, and use", Praeger Publishers, Westport CT (1986).

[5] Pinker, S. & Bloom, P. "Natural Language and natural selection", Behavioural and Brain Sciences **13**, 707-727 (1990).

[6] Chomsky, N. "Language and problems of knowledge", MIT Press, Cambridge, MA (1988).

[7] Shinbrot, T. & Young, W. Why decussate? - Topological constraints on neuronal wiring, development, and regeneration, Anatomical Record **291**, 1278-92 (2008).

[8] Chomsky, N., & Schützenberger, M., "The algebraic theory of contextfree languages", in *Computer Programming and Formal Systems*, Eds. Braffort, P., & Hirschberg, D., North Holland, Amsterdam, 118-161 (1963).

[9] Gazdar, G. & Pullum, G. "Natural Languages and Context-Free Languages", Linguistics and Philosoph **4**, 469-470 (1982).

[10] Shieber, S. "Evidence against the Context-Freeness of Natural Language", Linguistics and Philosophy **4**, 333-343 (1985).

[11] The string problem is undecidable, see Hopcroft, J., & Ullman, J. "Introduction to Automata Theory, Languages, and Computation", Prentice Hall, New Jersey, ISBN-10: 0321462254 / ISBN-13: 9780321462251 (2007).

[12] The numbers of orbits deviate from the numbers of *different* cumulative orbits exhibited in [2], but demonstrate the same tendency.

[13] Stoop, R., Stoop, N. & Bunimovich, L. "Complexity of Dynamics as Variability of Predictability", J. Stat. Phys. **114**, 1127-1137 (2004).

[14] Stoop, R. & Stoop, N. "Natural computation measured as reduction of complexity", Chaos **14**, 675-679 (2004).

[15] Cook, M. "Universality in Elementary Cellular Automata", Complex Systems **15**, 1-40 (2004).

[16] Schüle, M., & Stoop, R. "A full computation-relevant classification of the topological dynamics of elementary cellular automata", preprint (2011).

[17] Hofstadter, D. "Gödel, Escher, Bach: An Eternal Golden Braid", Basic Books, New York, ISBN 978-0465026562, ISBN 0140179976 (1979).

[18] Finch, T. "Three meanings of recursion", in "The Evolutions of Human Language", Eds. Larson, R., Déprez, V., & Yamakido, H. Cambridge University Press, Cambridge, ISBN 978-0521736251 (2010).