Are the neural circuits controlling the temporal structure of spontaneous actions involved several different behaviors?

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1. Introduction

Variability is an adaptive and ubiquitous feature of all our behaviors, which is actively regulated according to task demands. Behavioral variability explains why under similar circumstances, individuals will generate different actions. In humans at rest, the so-called default mode network (DMN) is activated, presenting characteristic, random-like activity fluctuations. Interestingly, remnants of these fluctuations in the suppressed DMN during a task explain much of the observed variability in the subject's behavior. The fruit fly Drosophila can show random-like behavior, the temporal structure of which is mathematically related to that of the DMN in humans. This behavioral variability can also be operantly conditioned. Therefore, research into the mechanisms of the brain circuits giving rise to behavioral variability and operant learning in *Drosophila* will provide insights that may prove crucial for our understanding the role of DMN in many psychiatric diseases. The goal is to identify and characterize the neural generators of this spontaneity in the fly and the effects of spontaneity on operant learning and vice versa. For this purpose, we use both a wing beat analyzer to record the spontaneous turning maneuvers of tethered flying *Drosophila* and a "*Drosophila* Joystick" to record spontaneous leg movements. This way, we can study and compare spontaneous behavioral variability in two completely different paradigms.
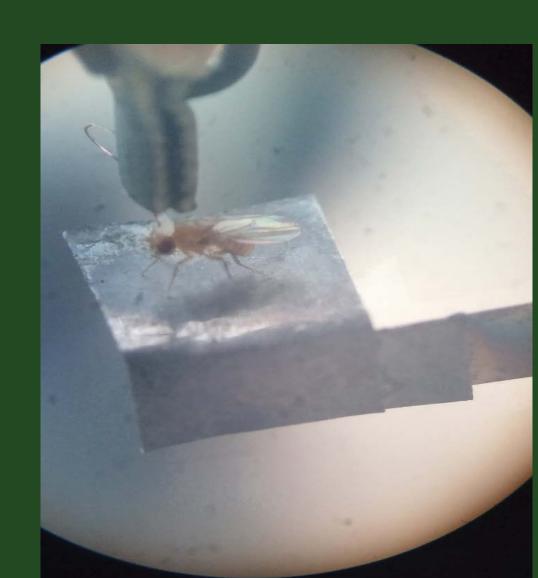
2. Apparatus

Joystick

Fig. 1. Joystick apparatus. A tethered fly is placed in a way so that it is standing upon a moveable platform. In this way, the fly can move the platform with its legs and push it to right or left. A photoelectric sensor is then detecting the position of the platform.

Wing beat analyzer

Fig. 2. Schematics of the wing-beat analyzer. A. The wing stroke amplitude is measured by tracking the wing shadows produced from an infrared LED on top of a suspended fly within the arena. Yaw turning is then calculated by subtracting the wing-beat amplitudes of the left and right wings. B. Alignment of the wing shadow (striped area) over the cutaway mask (grey area). The shadow cast by the wings was laterally centered over the cutaway mask.

Analysis

The S-map procedure (sequentially locally weighted global linear map) was used for the nonlinear prediction for the wing beat analyzer. It first creates a library set of vectors from the first half of the data. Then a single linearity parameter controls if the influence of the library vectors is linear or nonlinearly weighted by their respective distance to the vector used for the prediction.

Raw data from the Joystick were detrended by taking the first difference of the series for eliminating the short term correlations. The average mutual information (AMI) was used for estimating the embedding lag, thus taking into account nonlinear correlations.
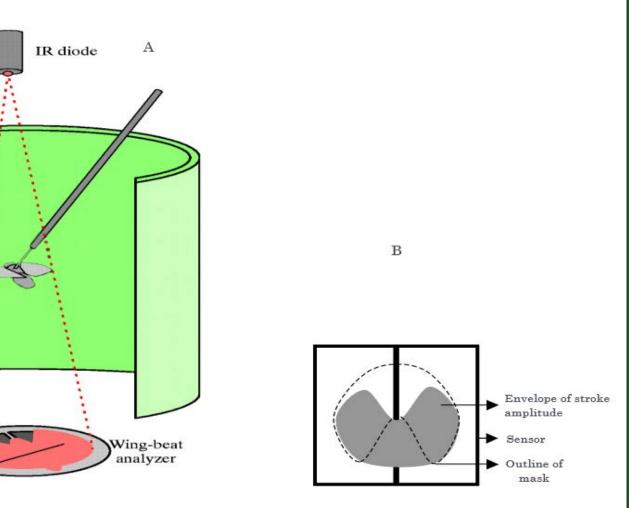
4. Summary

In the wing beat analyzer, we found a set of neurons that seem to be critical for the temporal structure of spontaneous turning behavior. We have started to compare and contrast these results with another, orthogonal behavioral modality. In addition, we applied different analysis algorithms as a way to test the generality of the flight findings. We could find evidence that nonlinear behavior is present in *Drosophila on the 'Joystick'*, and not only in turning behavior in the wing beat analyzer. However, the results from the 'joystick' experiment do not let us state this conclusion with complete confidence. Nuerons in the c105 and c232 drivers seem to work as a nonlinear generator in the wing beat analyzer, butnot in the 'joystick', indicating that the generators may be specific to the behavioral modality. However, our analysis of the behavior on the 'joystick' platform is too preliminary to allow for any firm conlusions.
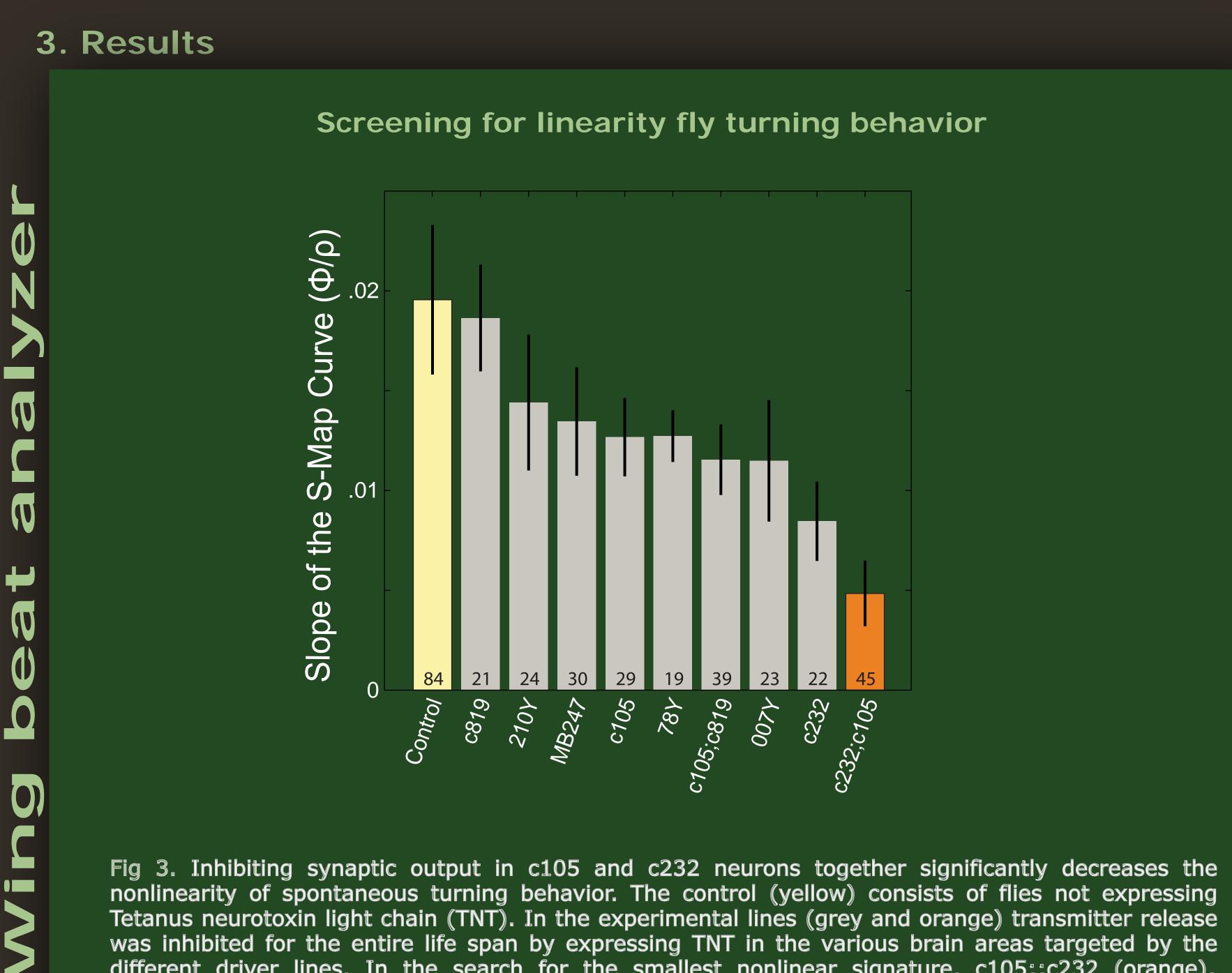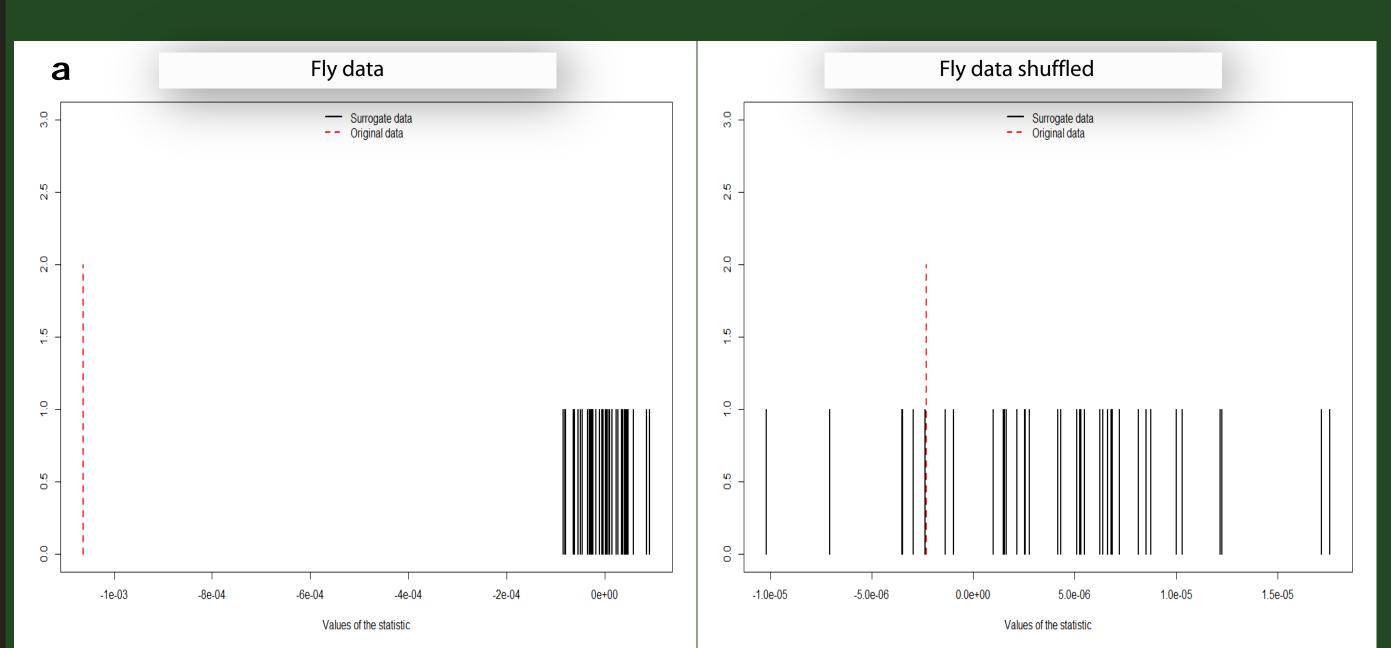
Wing beat analyzer

Joystick

3. Results

Screening for linearity fly turning behavior

Fig 3. Inhibiting synaptic output in c105 and c232 neurons together significantly decreases the nonlinearity of spontaneous turning behavior. The control (yellow) consists of flies not expressing Tetanus neurotoxin light chain (TNT). In the experimental lines (grey and orange) transmitter release was inhibited for the entire life span by expressing TNT in the various brain areas targeted by the different driver lines. In the search for the smallest nonlinear signature, c105;;c232 (orange), expressing in ellipsoid-body ring neurons shows the strongest effect.
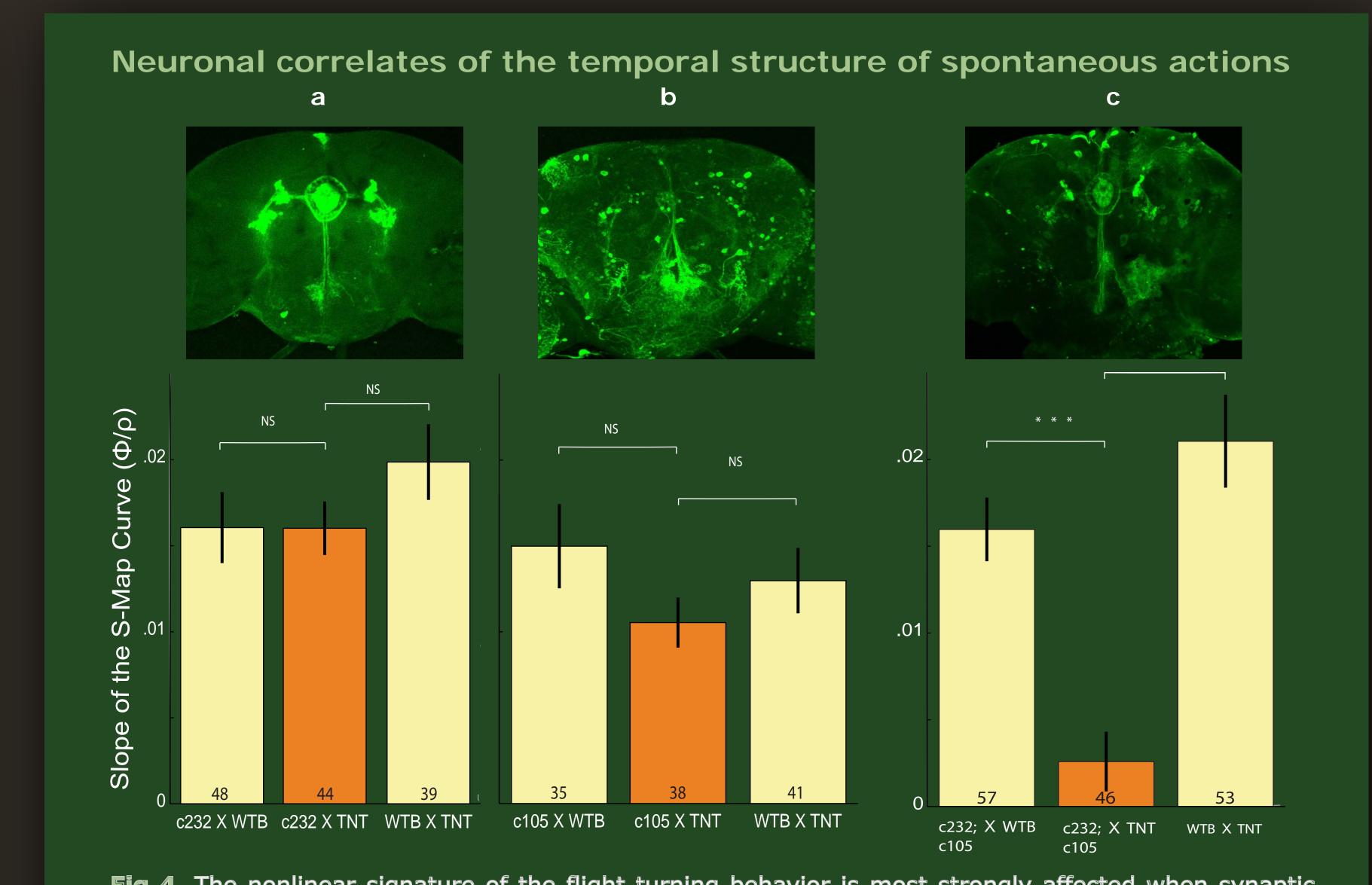
Neuronal correlates of the temporal structure of spontaneous actions

Fig 4. The nonlinear signature of the flight turning behavior is most strongly affected when synaptic output is blocked in both c105 and c232 neurons at the same time. Inhibiting the release of neurotransmitters in ech driver line alone does not have a significant effect on the S-Map curve slope (a, b). However, inactivation of both of them together reduces significantly the nonlinear signature (c). The images above each graph show the expression pattern of c232 (a), c105 (b), and of both drivers together (c).

Testing for memory with shuffled data

Fig 5. Fly behavior is not explained by a Gaussian linear process and nonlinearity can be assumed. Since linear stochastic series are symmetric under time reversal, this statistic is used for testing if the data was generated from a stationary linear stochastic process. For all of the flies tested (16), it shows a significant difference from the null hypothesis (a). However, nonstationarity or even random fluctuation of the test could be responsible of false positives. The surrogate data is generated by using a phase randomization procedure (maintaining mean and autocorrelation function of the original time series) (b). In addition the neural network tests of Teraesvirta and White and the Tsay test for nonlinearity show clear differences between the series generated by the flies from those from shuffling fly data (not shown).
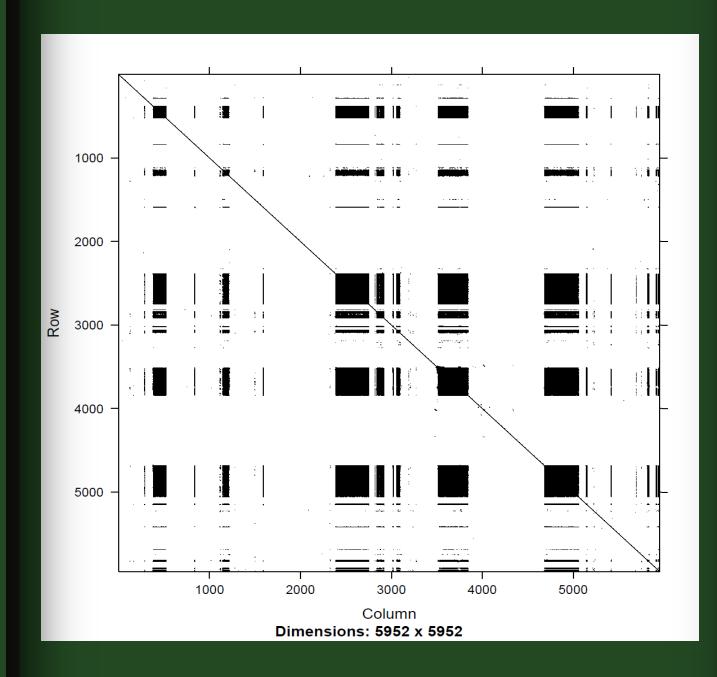
Recurrence plot

Fig 6. Representative recurrence plot of one of the tested flies. This is done by marking with dark points the near located neighbours of the reconstructed state space. The amount of successive dark points in the diagonal show how deterministic the series is (>0.9 for all the flies). In addition, an irregular pattern suggests that the time series is nonlinear. The quantitative data gathered from this plot did not show any clear differences among the groups.
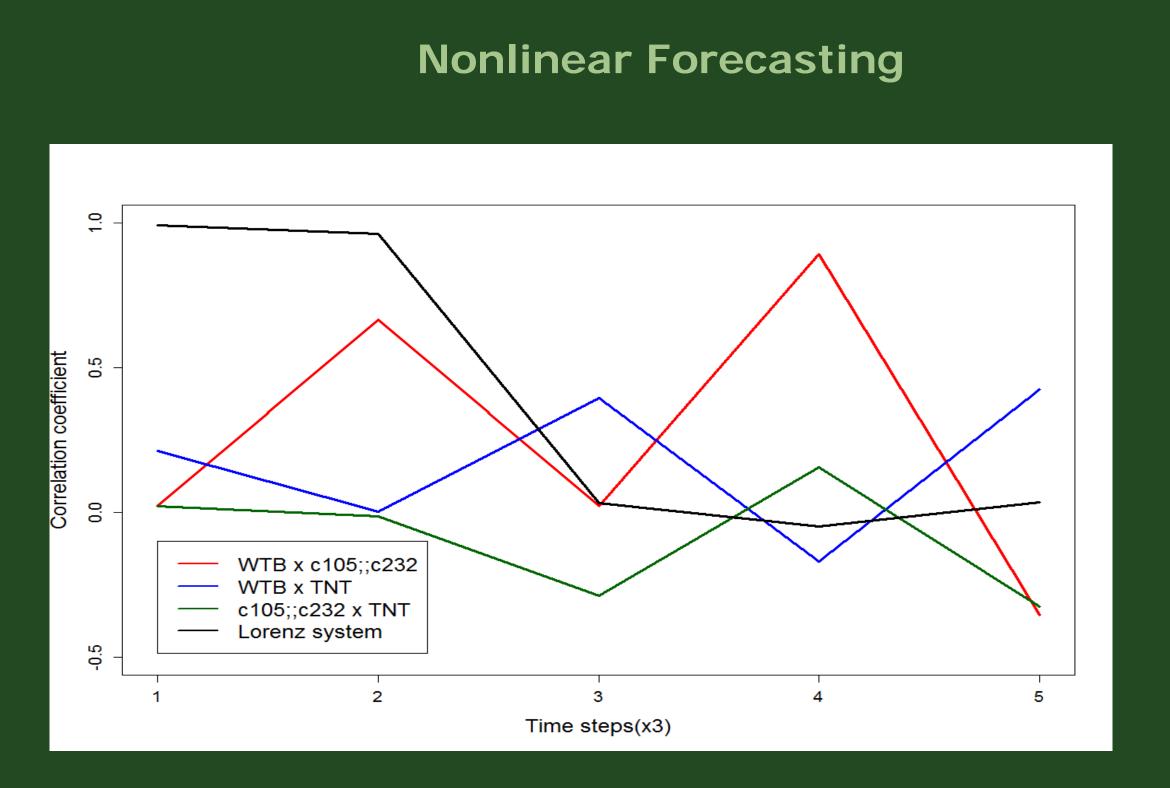
Nonlinear Forecasting

Fig 7. Nonlinear forecasting for the tested flies and the Lorenz chaotic system. Excluding the possibility of randomly generated uncorrelated (white) noise explaining the time series, the other possibility that has not been tested is correlated (colored) noise. The best way to overcome the problems associated with distinguishing linear stochastic processes from nonlinear deterministic ones, is nonlinear forecasting. Depending on the nature of the data, the correlation of predicted versus observed values show a different course for increasing forecasting intervals. In chaotic processes there is a fast decay of this correlation with time (as seen by the Lorenz system above). Interestingly, the nonlinear prediction of the the tested flies look rather like random uncorrelated noise.