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Symbolic dynamics of animal interaction

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ABSTRACT

Since its introduction nearly two decades ago, transfer entropy has contributed to an improved understanding of cause-and-effect relationships in coupled dynamical systems from raw time series. In the context of animal behavior, transfer entropy might help explain the determinants of leadership in social groups and elucidate escape response to predator attacks. Despite its promise, the potential of transfer entropy in animal behavior is yet to be fully tested, and a number of technical challenges in information theory and statistics remain open. Here, we examine an alternative approach to the computation of transfer entropy based on symbolic dynamics. In this context, a symbol is associated with a specific locomotory bout across two or more consecutive time instants, such as reversing the swimming direction. Symbols encapsulate salient locomotory patterns and the associated permutation transfer entropy quantifies the ability to predict the patterns of an individual given those of another individual. We demonstrate this framework on an existing dataset on fish, for which we have knowledge of the underlying cause-and-effect relationship between the focal subject and the stimulus. Symbolic dynamics offers an intuitive and robust approach to study animal behavior, which could enable the inference of causal relationship from noisy experimental observations of limited duration.

1. Introduction

Apprehending causal relationships in animal behavior is a pressing research question in the life sciences, with important consequences on our understanding of leader-follower interactions in social groups and fear response to predatory stimuli (King et al., 2009; Sumpter, 2010). Information theory has been proposed as a viable tool for unveiling causal relationships, promising an entirely data-driven approach to investigate animal behavior (Bartolini et al., 2016; Butail et al., 2014; 2016; Hu et al., 2015; Ladu et al., 2015; Mwaffo et al., 2017b; Neri et al., 2017; Orange and Abaid, 2015; Ruberto et al., 2016; Wang et al., 2012). Departing from traditional cross-correlation analysis (Krause et al., 2000; Ladu et al., 2014), information theory enables the study of nonlinear interactions subject to noise and unknown time-delays, without the need of an underlying model.

In an information-theoretic sense (Cover and Thomas, 2012), the information contained in a specific behavioral observation of an animal should be related to its degree of uncertainty. Information-rich behaviors comprise a constellation of locomotory bouts exhibited by the individual, while observations consisting of a single, repetitive, behavior will have limited information content. The seminal work of Paulus et al. (1990) offers a precise quantification of this idea in the context of locomotor activity of pharmacologically-manipulated rat, whose information content exhibits a dose-dependent response. Based on this theoretic interpretation of information, a causal relationship in the interaction between two animals could be revealed by an information transfer between them. In other words, we could say that a given stimulus, a conspecific or a predator, “causes” the behavior of a specific focal subject, if the uncertainty in predicting the future behavior of the focal subject is reduced by knowing the past behavior of the stimulus. The theoretic construct of transfer entropy, originally introduced by Schreiber (2000) to study interactions between time series, offers a precise, mathematically-grounded framework for this idea.

An excellent review on transfer entropy and its application to study information flow in technological and natural systems has been recent conducted by Bossomaier et al. (2016). For example, transfer entropy has been utilized to study functional connectivity networks in the brain (Vicente et al., 2011), cardiovascular and cerebrovascular regulations for early detection of syncope events (Faes et al., 2013), information flow between two financial time series (Marschinski and Kantz, 2002), and influential individuals in social media (Steeg and Galstyan, 2012). More recently, transfer

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entropy has been recently employed in political science to study policy-making in the United States of America, thereby measuring interactions between its 50 states (Anderson et al., 2016; Grabow et al., 2016).

In Butail et al. (2014), we first demonstrated the possibility of utilizing transfer entropy to study causal relationships in fish behavior from experimental observations. Within a new robotics-based experimental framework, we clarified the feasibility of detecting one-directional information transfer in social interactions in zebrafish (*Danio rerio*), a popular animal model in the life sciences (Orger and de Polavieja, 2017). Therein, the selection of the sampling time and the binning size were extensively investigated, based on the approach presented by Baptista et al. (2012), which offers a rigorous basis for the selection of computation parameters.

In Ladu et al. (2015), Bartolini et al. (2016) and Ruberto et al. (2016), we applied the same methodology to study the role of caffeine administration, body size, and motion pattern on the shoaling tendency of zebrafish. Experimental results in Ladu et al. (2015) indicate that intermediate and high caffeine concentrations result into a stronger influence of the robotic stimulus on the focal subject, which could be explained by the anxiety-related behavioral responses evoked by caffeine. Findings in Bartolini et al. (2016) demonstrate a differential effect of the size of the stimulus, which could be related to the fish tendency to take on leaders' role when shoaling with conspecifics of smaller size. In Ruberto et al. (2016), we have shown that information transfer in social interactions is modulated by the motion pattern of the stimulus, whereby three-dimensional movements of the robotic stimulus could enhance information flow.

The information-theoretic construct of transfer entropy has also been utilized by Hu et al. (2015) to study predator-prey interactions in fish. Findings therein suggest that the prey (rosy bitterling, *Rhodeus ocellatus*) is more vigilant than the predator (northern snakehead, *Channa argus*), whereby a net information flow is measured from the predator to the prey. Our recent work (Neri et al., 2017) offers further evidence on the possibility of applying transfer entropy to predator-prey interactions in fish, through a series of robotics-based controlled experiments on zebrafish. Beyond studies on fish, in Orange and Abaid (2015), transfer entropy has been successfully utilized to investigate social interactions in bats. Importantly, the authors found evidence for a higher transfer entropy from leading to following bats rather than from following to leading bats, which is in line with the theoretical expectation that information should propagate from the front to the rear of the group.

In a parallel line of work (Butail et al., 2016), we have demonstrated the possibility of identifying leader-follower relationships from synthetic, rather than experimental, data. The premise for using synthetic data was to minimize potential confounds associated with experimental uncertainties and provide a critical assessment for the use of transfer entropy in the study of animal behavior. Therein, we have considered a data-driven model of social behavior of zebrafish, based on the integration of two jump diffusion processes, simulating the turn rate dynamics of the subjects (Mwaffo et al., 2015). More recently, we have extended the approach to groups of fish, offering a robust methodology to integrate transfer entropy predictions with other approaches to network reconstruction in a maximum likelihood sense (Mwaffo et al., 2017b). Synthetic data have also been considered by Wang et al. (2012) to study information cascades in large groups of self-propelled particles in a three-zone model of swarming. The computation of transfer entropy presented therein uses relative position and heading variables to facilitate the detection of interactions from time series.

Despite the impressive breadth of studies supporting the use of transfer entropy in the inference of causal relationships, the practical computation of transfer entropy is a challenging task. The analyst has seldom access to exact probability density functions, whereby he/she relies on raw time series for transfer entropy estimation. In this process, the estimation of probability density functions of dimension equal to three is required for the triplet associated with the current states of the two processes and the state of one of them at the next time step. Modest perturbations due to experimental noise and limited samples size in relation to finite experimental time series could lead to large variances in transfer entropy estimates (Roulston, 1999), thereby hindering the validity of the inferred causal relationships.

For continuous distributions, two different approaches are mainly used to compute transfer entropy (Bossomaier et al., 2016; Hlaváčková-Schindler et al., 2007). The first one entails the use of kernel density estimation, which requires a large sample size along with the selection of a proper kernel-type function and a smoothing parameter. An inadequate choice of the kernel function and/or smoothing parameter may lead to inaccurate conclusions (Moon et al., 1995; Silverman, 1986). The second approach is the classical binning method, whose accuracy is determined by the sampling time and the binning size. The computation of transfer entropy based on the binning approach is highly sensitive to these parameters, whereby a poor selection may wash out interactions or magnify artificial correlations associated with inherent noise in the dataset.

Here, we examine an alternative approach to compute transfer entropy, based on symbolic analysis of ordinal patterns in the time series. Symbolic analysis is a field of increasing interest in several scientific disciplines (Amigó, 2010). It has foundations in information theory and in the theory of dynamical systems. The mathematical discipline of symbolic dynamics started in 1898 with the pioneering works of Hadamard (1898), who developed a symbolic description of sequences of geodesic flows, and was later extended by Morse (1921), who coined the name "symbolic dynamics." Collet and Eckmann showed that a complete description of the behavior of a dynamical system is captured in terms of certain, appropriate symbols (Collet and Eckmann, 2009). In the context of animal behavior, a symbol could be viewed as a locomotory bout that is identified from the time series of the motion of an individual. As a result, the motion of an individual is treated as a sequence of elementary locomotory bouts, which summarizes the behavior of the animal from its position or heading as previously proposed in the literature related to transfer entropy (Bartolini et al., 2016; Butail et al., 2014; 2016; Hu et al., 2015; Ladu et al., 2015; Mwaffo et al., 2017b; Neri et al., 2017; Orange and Abaid, 2015; Ruberto et al., 2016; Wang et al., 2012).

Computing transfer entropy from a limited set of symbols that measure animal behavior is a rather intuitive solution to the study of causal relationships in animal behavior, but its feasibility has never been tested. For example, it is tenable to hypothesize that a leader-follower interaction could be detected by examining the simple Boolean time series generated by annotating the time instants in which the animals suddenly invert their direction of motion, without requiring the precise quantification of their motion. The follower will be the individual in the pair which inverts its motion as a function of the leader behavior, while the leader should not be responsive to the follower. This exemplary computation would only require the computation of a three-dimensional probability density function with eight states, thereby dramatically enhancing our capability to make inference with experimental datasets of finite length. Also, consolidating the behavior into symbols is expected to reduce the role of experimental uncertainty, increasing the robustness of the inference. We demonstrate this approach on published experimental data from our group (Butail et al., 2014; Kim, 2017), which offer ground truth for testing our ability to correctly infer causal relationships.