Distinguishing states of conscious arousal using statistical complexity

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We apply techniques from the field of computational mechanics to evaluate the statistical complexity of neural recording data in fruit flies. We connect statistical complexity to the flies’ level of conscious arousal, which is manipulated by general anaesthesia (isoflurane). We show that the complexity of even single channel time series data decreases under anaesthesia. The observed difference complexity between the two conscious arousal states increases as higher orders of temporal correlations are taken into account. In contrast to prior work, our results show that complexity differences can emerge at very short time scales and across broad regions of the fly brain, thus heralding the macroscopic state of anaesthesia in a previously unforeseen manner.

I. INTRODUCTION

Complex phenomena are everywhere in the physical world. Typically, these emerge from simple interactions among elements in a network, such as atoms making up molecules or organisms in a society. Despite their diversity, it is possible to approach these subjects with a common set of tools, using numerical and statistical techniques to relate microscopic details to emergent macroscopic properties [1]. There has long been a trend of applying these tools to the brain, the archetypical complex system, and much of neuroscience is concerned with relating electrical activity in networks of neurons to psychological and cognitive phenomena [2]. In particular, there is a growing body of experimental evidence [3], that neural firing patterns can be strongly related to the level of conscious arousal in animals.

In humans, level of consciousness varies from very low in coma and under deep general anaesthesia to very high in fully wakeful states of conscious arousal [4]. Due to current limitations in discriminating these states, determining the level of conscious arousal based on neural activity is a clinically important problem in human society [5], and there is significant interest in developing reliable measurable proxies for it. In this context, neural recording data has been analysed using various techniques and notions of complexity [6] to try to find the most reliable measure of consciousness [6, 7].

One of the most successful techniques to date in distinguishing levels of conscious arousal is the perturbational complexity index [8–10], which measures the neural activity patterns that follows a perturbation of the brain through magnetic stimulation. The evoked patterns are processed through a pipeline then finally summarised using Lempel-Ziv complexity [9]. This method is inspired by a theory of consciousness, called integrated information theory (IIT) [11, 12], which proposes that a high level of conscious arousal should be correlated with the amount of so-called integrated information, or the degree of differentiated integration in a neural system (see Ref. [13] for details). While there are various ways to capture this essential concept [14, 15], one way to interpret integrated information is as the amount of loss of information a system has on its own future or past states based on its current state, when the system is minimally disconnected [16–18].

However, these complexity measures are motivated partly by phenomenological concerns and often make strong assumptions about the underlying process which are not necessarily borne out in reality. In particular, those based on IIT assume Markovian dynamics, i.e., that the future evolution of a neural system is determined statistically by its present state [15]. Moreover, IIT requires computing the correlations across all possible divisions between subsystems, which makes it computationally very hard. Given the importance of hierarchical information processing in the brain, manifesting as oscillations across a range of frequencies and spatial regions [19], it is likely that non-Markovian temporal correlations play a significant role in explaining any experimentally measurable behaviour. There is, therefore scope for applying more general notions of complexity to meaningfully distinguish macroscopic brain states.

A conceptually simple approach to quantifying the complexity of time series data, such as the fluctuating potential in a neuron, is to construct the minimal model which statistically reproduces it. Remarkably, there is a systematic procedure to find this minimal model, known as an epsilon machine (ε-machine), which has been developed within the field of computational mechanics [20, 21]. Crucially, ε-machines account for non-trivial temporal correlations contained in the data and can be used to quantify the statistical complexity of a process – the minimal amount of information required to specify its state. As such they have been applied in various fields, ranging from neuroscience [22, 23] and psychology [24] to crystallography [25] and ecology [26], to the stock market [27]. Lastly, unlike IIT the ε-machine analysis can be performed for data coming from a single channel.

In this paper, we use the statistical complexity derived from an ε-machine analysis of neural activity to distinguish states

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of conscious arousal in fruit flies (D. melanogaster) as induced by the presence or absence of anaesthesia (and confirmed through the flies behavioural response). We make use of existing neural data, taken from flies under different concentrations of isoflurane anaesthetic, which has already been analysed using conventional statistical tools in terms of noise spectra, coherence and Granger causality [28, 29]. By analysing signals from individual electrodes and disregarding spatial correlations, we find that statistical complexity distinguishes between the two states of conscious arousal through temporal correlations alone. Not only is it significantly lower in the anaesthetised state, but the difference in complexity increases with the degree of temporal correlations we include in our analysis. Moreover, where earlier analyses had indicated an impairment of central brain processing, we find the most significant reduction in complexity in peripheral brain regions, indicating a previously unidentified effect of anaesthesia. Before presenting these results in detail in Sec. III and discussing their implications in Sec. IV, we begin in the next section with a brief overview of the -machine framework we will use for our analysis.

II. -MACHINES AND STATISTICAL COMPLEXITY

To uncover the underlying statistical structure of neural activity that characterises a given conscious state, we treat the measured neural data, given by voltage fluctuations in time, as discrete time series. We detail how this is done in the next section. In this section, we outline the mathematical tools of computational mechanics, which will contribute to our analysis of these time series. We start by discussing how so-called -machines can be used as minimal models to explain stochastic data, before detailing how we construct them in practice. We then show how this can be used to extract a meaningful notion of complexity.

A. From time series to hidden Markov models

In abstract terms, a discrete-time series is a sequence of symbols \( r = (r_0, \ldots, r_k, \ldots) \) that appear over time, one after the other. Each element of \( r \) corresponds to a symbol from a finite alphabet \( \mathcal{A} \) observed at the discrete time step labelled by the subscript \( k \). The occurrence of a symbol, at a given time step, is random in general and thus the process, which produces the time series, is stochastic [30]. However, the symbols may not appear in a completely independent manner, i.e., the probability of seeing a particular symbol may strongly depend on symbols observed in the past. These correlations are often referred to as memory, and they play an important role in constructing models that are able to predictively describe the future behaviour of a given stochastic process [31].

Relative to an arbitrary time \( k \), let us denote the future and the past partitions of the complete sequence as \( \mathcal{r} = (\mathcal{r}, \vec{\mathcal{r}}) \), where the past and the future are \( \mathcal{r} = (\ldots, r_{k-2}, r_{k-1}) \) and \( \vec{\mathcal{r}} = (r_k, r_{k+1}, \ldots) \) respectively. In general, for the prediction of the immediate future symbol \( r_k \), knowledge of the past \( \ell \) symbols \( \vec{\mathcal{r}}_\ell := (r_k-\ell, \ldots, r_{k-2}, r_{k-1}) \), may be necessary.

The number of past symbols we need to account for in order to optimally predict the future sequence is called the Markov order [32]. A process is called Markovian if \( \ell = 0,1 \) and non-Markovian otherwise.

Memory effects complicate the construction of models that predict the future behaviour of processes. One way of characterising a non-Markovian process is by finding a hidden Markov model (HMM) that describes it [33]. These are predictive models with the capability to produce \( \vec{r} \) with statistics consistent with the observed past \( \mathcal{r} \). HMMs are Markov chains, which may be represented by digraphs [20, 32] \( G(V,E) \) consisting of a set of vertices \( v_i \in V \) and directed edges \( \{i,j\} \in E \), see Fig 1(c) and (d). In simple terms, a non-Markovian process is turned into a Markovian process via an HMM.

In general, the difficulty of modelling a time series, in terms of the number of conditional probabilities that must be accounted for, increases exponentially with its Markov order. However, not all pasts lead to unique future probability distributions, leaving room for compression in the model. Constructing a process’ HMM, which is not unique in general, requires accounting for the information, contained in \( \mathcal{r} \), necessary to predict \( \vec{r} \). Inefficient models consider the entire sequence, which may involve a high degree of redundancy. In a seminal work, Crutchfield and Young showed the existence of a class of HMM, which they called -machines, that are provably the optimal predictive models for a non-Markovian process under the assumption of statistical stationarity [20, 21]. Constructing the -machine is achieved by partitioning sets of partial past observations \( \mathcal{r} \) into causal states. That is, two distinct sequences of partial past observations \( \mathcal{r} \) and \( \mathcal{r} \) belong to the same causal state \( \mathcal{S} \), if the probability of observing a specific \( \mathcal{r} \) given \( \mathcal{r} \) or \( \mathcal{r} \) is the same: that is

\[
\mathcal{r} \sim \mathcal{r} \text{ if } P(\mathcal{r} | \mathcal{r}) = P(\mathcal{r} | \mathcal{r}),
\]

where \( \sim \) indicates that two histories correspond to the same causal state. The conditional probability distributions in Eq. (1) may always be estimated from a finite set of (statistically stationary) data via the naive maximum likelihood estimate, given by \( P(r_k|\mathcal{r}_\ell) = \nu(r_k,\mathcal{r}_\ell)/\nu(\mathcal{r}_\ell) \), where \( \nu(X) \) is the frequency of occurrence of sub-sequence \( X \) in the data. We now discuss how to practically construct an -machine for a given time series.

B. Constructing -machines with the CSSR algorithm

Several algorithms have been developed to construct -machines from time series data [20, 34, 35]. Here, we briefly detail the Causal State Splitting Reconstruction (CSSR) algorithm [24], which we use in this work to infer the minimal underlying HMM predicting the statistics of neural data we provide as input. For a more in-depth discussion of the algorithm and the parameters involved, a full treatment is given in Ref. [24].

The CSSR algorithm proceeds iteratively, constructing sets of causal states accounting for longer and longer subsequences of symbols. In each iteration, the algorithm first estimates the probabilities \( P(r_k|\mathcal{r}_\ell) \) of observing a symbol con-
ditional on each length $\ell$ prior sequence and compares them with the distribution $P(r_k|S = S_i)$ it would expect from the causal states it has so far reconstructed. If $P(r_k|\bar{r}_k) = P(r_k|S = S_i)$ for some causal state, then $\bar{r}_k$ is identified with it. If the probability is found to be different for all existing $S_i$, then a new causal state is created to accommodate the sub-sequence. By constructing new causal states only as necessary, the algorithm guarantees a minimal HMM that describes the non-Markovian behaviour of the data (up to a given memory length), and hence the corresponding $\epsilon$-machine of the process.

The CSSR algorithm compares probability distributions via the Kolmogorov-Smirnov (KS) test [36, 37]. The hypothesis that $P(r_k|\bar{r}_k)$ and $P(r_k|S = S_i)$ are identical up to statistical fluctuations is rejected by the KS test at the significance level $\sigma$ when a distance $D_{KS}$ [38] is greater than tabulated critical values of $\sigma$ [39]. In other words, $\sigma$ parametrises the probability that an observed history $\bar{r}_k$ belonging to a causal state $S_i$, is mistakenly split off and placed in a new causal state $S_j$. As is discussed in Ref. [24], the choice of this value minimally affects the convergence properties of the algorithm. As a result, we set $\sigma = 0.005$ for the entirety of this study unless stated otherwise.

As it progresses, the CSSR algorithm compares future probabilities for longer and longer sub-sequences, up to a maximum past history length of $\lambda$. Aside from $\sigma$, this is the only important parameter that must be selected prior to running CSSR, and which affects the overall structure of the resulting $\epsilon$-machine. The choice for a value of $\lambda$ corresponds to the largest size of memory we are willing to consider in a stochastic process corresponding to a given time series. For a stochastic process of Markov order $\ell$, choosing $\lambda < \ell$ means that the long-memory structures present in the data are not captured by the inferred $\epsilon$-machine. Despite this, the CSSR algorithm will still produce an $\epsilon$-machine that is consistent with the approximate future statistics of the process up to order-$\lambda$ correlations [24]. This effect is one-sided, since choosing $\lambda \geq \ell$ guarantees convergence on the true $\epsilon$-machine given sufficient data. One important caveat to note is that the time complexity of the algorithm scales asymptotically as $O(2^{\lambda+1})$, putting an upper limit to the longest history length that is computationally feasible to use.

Furthermore, the finite length of the time series data implies an upper limit on an ‘acceptable’ value of $\lambda$. Estimating $P(r_k|\bar{r}_\lambda)$ requires sampling strings of length $\lambda$ from the finite data sequence. Since the number of such strings grows exponentially with $\lambda$, choosing maximum memory length $\lambda$ that is too long relative to the size $N$ of the data, provides a severely under-sampled estimation of the distribution. A distribution $P(r_k|\bar{r}_{\lambda_{\text{max}}})$ that has been estimated from an under-sampled space is almost always never equal to $P(r_k|S = S_i)$, resulting in the algorithm creating a new causal state for every string of length $\lambda$ it encounters. A bound for the largest permissible history length is $L(N) \geq \log_2 N / \log_2 |A|$, where $L(N)$ denotes maximum length for a given data size of $N$ [40, 41]. Once these considerations have been taken into account, the $\epsilon$-machine produced by the algorithm provides us with a meaningful quantifier of the complexity of the process generating the time series, as we now discuss.

### C. Statistical complexity of a process

The output of the CSSR algorithm is the set of causal states and rules for transitioning from one state to another. Using these rules, one can find the probabilities $P(S_i)$ to find the $\epsilon$-machine in each of the causal states at a randomly chosen time. The Shannon entropy of this distribution quantifies the minimal number of bits of information required to optimally predict the future process; this measure, first introduced in Ref. [20], is called the statistical complexity:

$$C_\mu := H[S] = -\sum_i P(S_i) \log P(S_i).$$

When Refs. [20, 21] describe $\epsilon$-machines to be provably optimal HMMs, it is with respect to $C_\mu$.

While a variety of alternative definitions and measures of complexity have been proposed in the literature (Ref. [42] contains a list of 386 such measures), the properties of $C_\mu$ allow for well-defined interpretations in terms of temporal structure [43]. It is important to note that the statistical complexity, as defined in Eq. (2), is zero for both deterministic and uniformly random processes; it is largest for stochastic processes with large memory effects. In the next section, we show that the statistical complexity of the neural time series for the conscious arousal states of the fly corresponding to awake and anaesthetised conditions are significantly different.

### III. COMPLEXITY IN NEURAL DATA

#### A. Neural time series

In this section, we analyse local field potential (LFP) data from the brains of awake and isoflurane-anaesthetised *D. melanogaster* (Canton S wild type) flies. This data was previously analysed in Ref. [29], and we will compare and contrast our results with earlier findings below. Here, we briefly review the main experimental details and refer the reader to Refs. [28, 29] for the full experimental description. LFPs were recorded by inserting a linear silicon probe (Neuronexus 3mm-25-177) with 16 electrodes separated by 25 $\mu$m. The probe covered approximately half of the fly brain and records neural activity from both peripheral and central brain structures, as illustrated in Fig. 1(a). A tungsten wire inserted into the thorax acted as the reference. The LFPs at each electrode were recorded for 18s while the fly was awake and 18s more when the fly was anaesthetised. The latter condition was induced by delivering isoflurane anaesthesia, 0.6% by volume, through an evaporator. Flies’ unresponsiveness during anaesthesia was confirmed by the absence of behavioural responses to a series of air puffs, established through analysis of video recordings of the experiment.

We used data sampled at 1kHz for the analysis [28], and to obtain an estimate of local neural activity, the 16 electrodes were re-referenced by subtracting adjacent signals giving 15 channels which we parametrise as $c \in [1, 15]$. Line noise was removed from the recordings, followed by linear de-trending...
and z-scoring, removing the mean and dividing by the standard deviation. The resulting data is a fluctuating voltage signal, which is time-binned and binarised, leading to a time series, see Fig. 1(b).

For each of the 13 flies in our dataset, we have 30 time series of length \( N = 18,000 \). They correspond to the 15 channels, labelled numerically from most peripheral to most central and depicted in Fig. 1(a), and the two states of conscious arousal. Using the CSSR algorithm [24], we constructed \( \varepsilon \)-machines for each of these time series as a function of maximum memory length within the range \( \lambda \in [2, 11] \). This is well below the memory length \( L(N) \sim 14 \) beyond which we would be unable to reliably determine transition probabilities for a sequence of length \( N = 18,000 \) [45]. We recorded the resulting 3,900 \( \varepsilon \)-machine structures, and corresponding statistical complexities, and grouped them according to their respective conscious arousal state. We present the results in the following sections.

B. \( \varepsilon \)-machines distinguish between states of conscious arousal

In order to observe the effects of isoflurane on neural complexity, we begin by visually inspecting the HMMs of the \( \varepsilon \)-machines for corresponding to the two levels of conscious arousal. We are interested in observing differences in the visual characteristics of the two \( \varepsilon \)-machines heralding the two levels of conscious arousal. Here, memory length \( \lambda \) plays an important role. For \( \lambda \leq 2 \) we do not expect to observe many distinguishing features between \( \varepsilon \)-machines corresponding to different external conditions. Given the finite alphabet \( \mathcal{A} \), the maximum number of causal states that may be generated at a given \( \lambda \) scales according to \( |\mathcal{A}|^|\lambda| \) [24]. In our case, the alphabet is binary, \( \mathcal{A} = \{0, 1\} \). This greatly restricts the space of non-Markovian \( \varepsilon \)-machine configurations available for short history lengths [46]. For \( \lambda = 1 \), we observe exactly one \( \varepsilon \)-machine configuration for all flies, channels and the states of conscious arousal. For \( \lambda = 2 \) we observe four distinct configurations. In contrast, the range \( \lambda \geq 3 \) allows for the extent of the memory correlations to be considered over longer time intervals, increasing the potential for the \( \varepsilon \)-machines in-
ferred from wakeful data to represent more complex neural time series, compared to $\epsilon$-machines inferred from data with anaesthetised flies.

We observe this distinction visually; it is marked by an increased number of inferred causal states and transitions, in addition to an apparent increase in overall graph connectivity, for wakeful data. The directed graphs shown in panels (c) and (d) of Fig. 1 demonstrate a typical example of the observed visual distinctions present between $\epsilon$-machines. Both depicted HMMs are the $\epsilon$-machines inferred from the channel 1 data recordings of fly 1, at maximum memory length $\lambda = 3$. The 4-causal state $\epsilon$-machine shown in Fig. 1(c), correspond to the anaesthetised time series, while the 8-causal state $\epsilon$-machine depicted in Fig. 1(d) corresponds to the wakeful data. The reduction in graphical complexity for the $\epsilon$-machine in the anaesthetised case is a result that is consistent with the majority of observed cases.

While this implies that of the two conscious arousal states, the wakeful state exhibits a higher statistical complexity than the anaesthetised one, the graphical differences become increasingly difficult to describe with growing maximum memory length. Furthermore, we cannot draw meaningful conclusions by only examining the visual features of 3,900 graphs. Instead, we quantitatively compare the statistical complexities of the two states for otherwise similar conditions by taking the difference between them

$$\Delta C_{\mu} = C_{\mu}^{\text{wake}} - C_{\mu}^{\text{anaes}},$$

this is an implicit function of the set of parameters \{\lambda, f, c\}, where \(f\) and \(c\) label the particular fly and channel respectively. We always consider $\Delta C_{\mu}$ for fixed values of \{\lambda, f, c\} on both sides of the equality. Positive values of $\Delta C_{\mu}$ indicate higher complexities observed in the wakeful state than in the anaesthetised one, and larger magnitudes correspond to clearer distinctions between them. Although there is expected to be a variation in raw statistical complexity across flies within the same level of conscious arousal, $\Delta C_{\mu}$ shields against this problem by considering only the relative differences between the conscious arousal states of the individuals.

Equipped with this measure, we analyse the effects of isoflurane on complexity as follows. We make use of the notation $\langle \langle \Delta C_{\mu} \rangle \rangle_p$ to denote taking an average of $\Delta C_{\mu}$ over parameter \(p \in \{\lambda, f, c\}\). To start with, we take the average of statistical complexity differences over all channels $\langle \langle \Delta C_{\mu} \rangle \rangle_c$ in order to neglect variations across different brain regions and focus solely on the effect of memory length. We then compute a pooled mean $\langle \langle \Delta C_{\mu} \rangle \rangle_f$, by taking the average over all flies (\(n = 13\)), leaving maximum memory length $\lambda$ as the only free parameter. Calculating the pooled mean at each maximum memory length $\lambda \in [1, 11]$, we obtain the 95% confidence intervals over the sample corresponding to $\langle \langle \Delta C_{\mu} \rangle \rangle_f \neq 0$, by calculating the standard error of the pooled mean and multiplying by the inverse $t$-distribution.

We observe a significant distinction in the statistical complexity between conscious arousal states for all maximum memory lengths $\lambda \geq 3$, marked by the pooled mean yielding significantly positive values $\langle \langle \Delta C_{\mu} \rangle \rangle_f > 0$. In this region, isoflurane is shown, on average, to reduce the statistical complexity of neural time series for flies, although some exceptions are present for a small subset of individuals. As mentioned in Sec. II, selecting a maximum memory length greater than the Markov order of the process will saturate the number of causal states inferred by CSSR [24]. It is likely that the tested \(\lambda\) range remains below the Markov order of the neural data, indicated by the lack of a plateau in statistical complexity. Nevertheless, Fig. 2 demonstrates that saturation of Markov order is not required for discrimination between conscious arousal states.

C. Complexity mapped in the fly brain

In the previous section, we established the capability for $\epsilon$-machines to distinguish between hemisphere-wide states of conscious arousal by observing significantly positive channel and fly averaged statistical complexity differences over the entire sample. However, neurological studies make it clear that the central and peripheral regions in the fly brain are affected asymmetrically by isoflurane, due to their distinct roles in stimulatory processing [28, 29, 47–49]. Most notably, Refs. [28, 29] showed that the correlations between central and peripheral regions experienced the greatest reductions, especially at lower frequencies. Given this information, it is natural to question whether or not the results observed in Sec. III B depend on the central-peripheral regions in the same manner.

To test the effect of channel location on the conscious arousal state, we examine $\langle \Delta C_{\mu} \rangle_f$ for each value of \(c\). This quantity characterises the average change in statistical complexity experienced by each brain region when subjected to
isoflurane gas. Determining \( \langle \Delta C_\mu \rangle_f \) only for \( \lambda = 11 \), we position this analysis in the region that demonstrates the clearest distinctions between conscious arousal state in Fig. 2.

As shown in Fig. 3, we find that isoflurane reduces statistical complexity most strongly for channels 1 to 7, corresponding to peripheral regions of the brain, indicated by the larger quantity of channels with \( \langle \Delta C_\mu \rangle_f > 0 \) above significance. In addition, the grouped periphery (channels 1 to 7), is observed to exhibit higher mean statistical complexity \( \langle \langle \Delta C_\mu \rangle_f \rangle_{c:1:7} = 0.65 \) compared to the grouped centre (channels 9 to 15), \( \langle \langle \Delta C_\mu \rangle_f \rangle_{c:9:15} = 0.35 \).

Interestingly, these results capture a complementary effect of anaesthesia to those presented in Refs. [28, 29]. They define power spectra as the distribution of the awake and anaesthetised time series in the frequency domain, and analysed over the grouped periphery and the central channels. A principal observation in Ref. [29] was the suppression of power spectra in low-frequency signals in central and peripheral regions. In the peripheral group, differences in power between the two levels of conscious arousal were less significant higher frequencies but persisted for all frequencies between the two levels of conscious arousal were less significant.

where this region is the only memory length which contains more detail, we first argue for their statistical significance. Before discussing the broader implications of our results in more detail, we first argue for their statistical significance.

**D. Significance analysis of results**

To locate the statistically significant regions in the parameter space formed by maximum memory length and channel number, we map it according to the significance of a statistical hypothesis test. We use the one-sample \( t \)-test to evaluate the statistical significance of the \( \Delta C_\mu \) observations over the sample of flies. Following the notation used in the previous sections, the \( t \)-statistic under this location test is given by

\[
t = \frac{\langle \Delta C_\mu \rangle_f - \mu_0}{s_\mu / \sqrt{n}}
\]

where \( \langle \Delta C_\mu \rangle_f \) represents the sample mean of \( C_\mu \), \( \mu_0 \) is the population mean of the null hypothesis, \( s_\mu \) is the sample standard deviation, and \( n \) is the sample size.

In our case, the null hypothesis corresponds to \( \mu_0 = 0 \), indicating no effect of isoflurane on the complexity between wakeful and anaesthetised neural time series. We calculate the critical values of the test statistic \( t_{\text{crit}} \) that reject this null hypothesis at significance level \( \alpha = 0.05 \) by using the inverse \( t \)-distribution

\[
t_{\text{crit}} = t_{\text{inv}}(\alpha, \text{d.o.f}),
\]

with degrees of freedom d.o.f = \( n - 1 = 12 \). We report the two-tailed critical values \( t_{\text{crit}} = \pm 2.1788 \). Since we are interested in the \( (c, \lambda) \) pairings that yield results that are anomalous with respect to the null population mean, we emphasise that we obtain \( \langle \Delta C_\mu \rangle_f \) by calculating the fly-averaged differences in statistical complexity. In doing so, we ensure that the test statistic is sensitive only to the effect of isoflurane on each fly, rather than the relative complexities that exist between the individuals. Accounting for \( \langle \Delta C_\mu \rangle_f \) in this way, we plot the \( t \)-statistic as a colour map over parameter space in Fig. 4.

We find that although the majority of the significance map is directed towards positive values of the \( t \)-statistic, only a subset of cells in \( (\lambda, c) \) space contain values above the upper bound specified by \( t_{\text{crit}} \). Exceptions are observed for \( \lambda = 2 \), where this region is the only memory length which contains points in the parameter space that are significantly below the lower bound on \( t_{\text{crit}} \). These cases correspond to regions where the statistical complexity of the neural time series under anaesthesia is greater than the wakeful series. While this observation marks this history length as anomalous relative to the others, it is likely that this effect is due to the small potential for large variations in \( \Delta C_\mu \), as was discussed in Sec. III B (compare with Fig. 2 at \( \lambda = 2 \) [50].

The most central channel \( (c = 15) \) presents another region of interest. Unlike other channels, where the \( t \)-statistic appears to become significant \( t > t_{\text{crit}}^+ = \pm 2.1788 \), as history earlier results can be interpreted as a reduction of higher level brain function in the anaesthetised state of conscious arousal, our analysis indicates that isoflurane also decreases short time-scale complexity in regions that are thought to lie lower in the information processing hierarchy [29, 47–49].

**Figure 3. Statistical complexity mapped throughout the fly brain.** The dashed line marks the observed differences between states of conscious arousal. The positive y-axis indicates higher complexity in wakeful data compared to anaesthetised data. The solid colour line corresponds to statistical complexity differences in each channel, averaged over all flies \( \langle \Delta C_\mu \rangle_f \), computed at maximum memory length \( \lambda = 11 \), and with error bars corresponding to the 95% confidence intervals over the fly sample \( (n = 13) \). Grey lines represent complexity differences for a single fly, performed at the same history length.
length becomes long $\lambda > 9$, the $t$-statistic is directed negatively, hinting that the statistical complexity of neural time series within this region are on average greater in the anaesthetised state. However, these negatively directed scores are weak and fall within the critical region, thus remaining consistent with the null hypothesis. This observed behaviour for channel 15 further supports our findings in Sec. III C by confirming that maximum memory length is not sufficient to distinguish between levels of conscious arousal in the central regions.

Excepting the case $\lambda = 2$, we observe regions of significantly positive $t$-scores for larger maximum memory lengths $\lambda \sim 10$ and 11. The mid-hemisphere channels spanning the range 5 to 7 elicit the strongest differences between levels of conscious arousal, indicative of a highly significant $t > t^\text{crit}_\text{+}$ region for almost all maximum memory lengths greater than 2. Channel 9 is also observed to host a similar region, but for $\lambda > 5$. This observation identifies the mid-hemisphere region in the fly brain as particularly sensitive to complexity changes between conscious arousal states.

**IV. CONCLUSIONS**

We have studied the complexity of neural recordings in the brains of flies in two states of conscious arousal: awake and anaesthetised. We have demonstrated that information about these macroscopic conditions is present in the statistical complexity of local electrical fluctuations in various brain regions. Specifically, we analysed the single-channel signals from electrodes embedded in the brain using the $\epsilon$-machine formalism, and quantified the statistical complexity of the recorded data for 15 channels in 13 flies in two conscious arousal states. We found the statistical complexity to be larger on average when a fly is awake than when the same fly is anaesthetised. The measured difference in complexity is present across the majority of the brain regions, it is present even at the smallest non-trivial memory lengths ($\lambda > 2$), and continues to grow as longer temporal correlations are taken into account; the trend suggests that we are far from saturating the Markov order of the process and with more data we would be able to further distinguish between the two states.

We have compared and contrasted our findings with other univariate single channel measures. In particular, Ref. [29] analysed the same dataset using power spectra and found that the central region of the brain is more sensitive to anaesthesia at lower frequencies. This means the correlations between two temporal points are more significantly reduced when they are further apart in time. In contrast, the $\epsilon$-machine analysis here accounts for higher order temporal correlations (up to 11-point correlations when $\lambda = 11$), which have a much richer structure in general. On the other hand, while our results are limited to higher frequencies, we still observe significant effects of anaesthesia. This suggests that other measures of complexity might be able to identify further structures that are affected by anaesthesia at different spatial and temporal scales. It is likely that applying a similar analysis to other datasets, in particular, human EEG data will lead to new discoveries regarding the relationship between consciousness and complexity that can be retrieved simply at the single channel level.

We are in the process of analysing the same data with IIT [51], which will provide the basis for a future comparison between the IIT and $\epsilon$-machine approaches, and the importance of going beyond the Markov assumption. Nevertheless, a key advantage of the present approach over IIT is that the $\epsilon$-machine analysis can be performed with the data from a single channel, while IIT requires data from two or more channels to assess the level of integration. However, interestingly, the single channel analysis here already contains some information about the multiple channels due to the concept of Sugihara causality [52]. This is because any one region of the brain is causally interacting with the rest of the brain, the temporal correlation in single channel time series contains information about spatial correlations, i.e., information that would be contained in multiple channels. With this logic, Ref. [53] infers the complexity of the multi-channel interactions from a single channel temporal structure of the time series.

Still, it would beneficial to extend the present analysis to the multi-channel scenario since such an $\epsilon$-machine can be subjected to the methods of IIT by cutting across channels. This approach has further advantages because it may help to discover the states and mechanisms of a system from the intrinsic viewpoint. IIT’s general prescription is to try out all possible states and mechanisms and to find out the states and mechanisms that maximise the integrated information. On the other hand, an $\epsilon$-machine, especially in single-channel based analysis can be first used to identify the reasonable history length for each channel, and then regard the states of the corresponding length as a minimal unit of temporal sequence.

Discovering a reliable measure of conscious arousal in an-
imals and humans remains one of the major outstanding challenges. The present study takes this challenge by connecting a complexity measure to the degree of conscious arousal. Our study here is a step forward to strengthening the link between physics, complexity science, and neuroscience. Here we have taken tools from the former and have applied them to a problem in the latter. Indeed there is a flow of ideas going the other way as well [54–56]. Our interdisciplinary study opens up new possibilities; physics can improve its theoretical constructs through the application of tools to empirical data, while neuroscience can benefit from rigorous quantitative tools that have proven its physical basis across different spatio-temporal scales.

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