

Spiral defect chaos with intermittency increases mean termination time

Mahesh Kumar Mulimani^{1,*} and Wouter-Jan Rappel^{1,2,†}

¹*Department of Physics, University of California San Diego, La Jolla, California 92093, USA*

²*Department of Bioengineering, University of California San Diego, La Jolla, California 92093, USA*



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Cardiac models are examples of excitable systems and can support stable spiral waves. For certain parameter values, however, these spiral waves can become unstable, resulting in spiral defect chaos (SDC), characterized by the continuous creation and annihilation of spiral waves and thought to underlie atrial fibrillation. During SDC, the number of spiral waves fluctuates and drops to zero at termination. In this work, we demonstrate that varying a single parameter allows the system to transition from SDC to a single spiral wave, passing through an intermediate regime of intermittency. In such intermittent dynamics, intervals of SDC are sandwiched between non-SDC intervals during which the number of spiral waves remains small and constant. We quantify this intermittency and show that the mean termination time increases significantly as the control parameter approaches values for which a single spiral wave is stable. In addition, we observe that quasistable spiral waves may intermittently persist in part of the computational domain, while the rest of the domain exhibits SDC. Our results may have implications for clinical atrial fibrillation, which often shows intermittency, switching back-and-forth between fibrillation and normal sinus rhythm.

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I. INTRODUCTION

Spiral defect chaos (SDC) is a ubiquitous dynamical process in spatially extended excitable media that involves the continuous creation and annihilation of spiral waves. It is observed in oscillatory Belousov-Zhabotinsky chemical reactions [1,2], in fluid dynamics such as the Rayleigh-Bernard convection cells [3], and in model systems such as the complex Ginzburg-Landau equation [4]. In addition to these physical systems, SDC is observed in cardiac tissue where it is believed to underlie dangerous and potentially lethal arrhythmias [5–13]. For example, atrial fibrillation (AFib), the most prevalent cardiac arrhythmia, is thought to be driven by spiral waves that are self-regenerating. During AFib, the electrical activation of the heart is disordered. AFib can occur in patients for just a few minutes, after which normal sinus rhythm is restored, or persist for months or even longer at a time. [14–17]. This difference in time scales is also reflected in the clinical classification of AFib: paroxysmal atrial fibrillation (AFib) is defined as an arrhythmia that lasts less than seven days and typically resolves on its own while persistent AFib refers to arrhythmias that last more than seven days and often require medical intervention to restore normal sinus rhythm [18,19]. In addition to paroxysmal fibrillation, patients can also exhibit alternating periods between AFib and atrial flutter, characterized by more ordered activation patterns [20–22].

The propagation of activation waves in cardiac tissue can be simulated using electrophysiological models, which formulate the membrane voltage of cardiac cells in terms of a set

of coupled equations [12,13]. These models are excitable and, by breaking the wavefront, it is possible to create a single spiral wave. For certain model parameters, however, this single spiral wave is unstable, resulting in the stochastic creation and annihilation of spiral waves and SDC [23]. Numerical studies of these models have demonstrated that the number of spiral tips in SDC is a stochastic quantity and that its birth-death process can be cast into a master equation, a commonly used approach in the field of population dynamics [24–26]. Using this master equation, it is possible to show that there is a finite probability of spiral wave termination and that the resulting termination times are exponentially distributed [27]. This is consistent with the clinical finding that fibrillation involves the creation and annihilation of spiral waves with interevent times obeying a Poisson renewal process [28]. Furthermore, numerical studies also showed that the mean termination time, T_{term} , depends critically on the size of the simulation domain. More specifically, it was shown that T_{term} increases exponentially with the domain size. This aligns with clinical findings, which show that larger hearts have a higher risk for AFib [29–31].

In this study, we show that increasing the domain size is not the only way to increase the mean termination time. We show that for certain parameter sets, a generic cardiac model can exhibit intermittency, which can greatly increase T_{term} . During this intermittency, periods of SDC, characterized by the stochastic creation and annihilation of spiral waves, are sandwiched between periods during which the system exhibits a small and stable number of spiral waves. We demonstrate that the duration of these non-SDC periods can be prolonged by adjusting a model parameter, leading to a substantial increase in the mean termination time. It is important to note here that, the transition from SDC to the non-SDC is due to the internal dynamics and not driven by perturbations as there are

*Contact author: mmulimani@ucsd.edu

†Contact author: rappel@physics.ucsd.edu

TABLE I. FK-model parameters used in our simulations. The parameter in bold face, τ_{-w} , is varied within the indicated range.

Parameter name	Parameter value
τ_v^+	3.3 ms
τ_{-v1}	12 ms
τ_{-v2}	2 ms
τ_{+w}	1000 ms
τ_d	0.36 ms
τ_0	5 ms
τ_r	33 ms
τ_{si}	29 ms
k	15
u_c^{si}	0.7
u_c	0.13
u_v	0.04
τ_{-w}	50–300 ms

no perturbations applied to the system. It is important to note here that the transition from SDC to the non-SDC is due to the internal dynamics and not driven by perturbations applied to the system. We also mention here that the termination of chaotic wave activity is often referred to as the transient chaos, corresponding to a chaotic saddle in the phase space [32–34].

II. METHODS

A. Electrophysiological model

We use the Fenton-Karma (FK) model, a widely used cardiac model [35], for our study. The FK model consists of three variables: the variable u that represents transmembrane potential, the fast gating variable v , and the slow gating variable w . These variables obey the following PDE and ODEs:

$$\frac{\partial u}{\partial t} = D\nabla^2 u - [J_{fi}(u, v) + J_{so}(u) + J_{si}(u, w)], \quad (1)$$

$$\frac{\partial v}{\partial t} = \frac{\Theta(u_c - u)(1 - v)}{\tau_v^-(u)} - \frac{\Theta(u - u_c)v}{\tau_v^+}, \quad (2)$$

$$\frac{\partial w}{\partial t} = \frac{\Theta(u_c - u)(1 - w)}{\tau_{-w}} - \frac{\Theta(u - u_c)w}{\tau_{+w}}, \quad (3)$$

$$J_{fi}(u, v) = -\frac{v}{\tau_d} \Theta(u - u_c)(1 - u)(u - u_c), \quad (4)$$

$$J_{so}(u) = -\frac{u}{\tau_0} \Theta(u_c - u) + \frac{1}{\tau_r} \Theta(u - u_c), \quad (5)$$

$$J_{si}(u, w) = -\frac{w}{2\tau_{si}} (1 + \tanh[k(u - u_c^{si})]), \quad (6)$$

$$\tau_v^-(u) = \Theta(u_v - u) \tau_{-v2} + \Theta(u - u_v) \tau_{-v1}, \quad (7)$$

where C_m (μFcm^{-2}) is the membrane capacitance, the diffusive term expresses the intercellular coupling via gap junctions and diffusion constant D , J_{si} and J_{so} are slow-inward and slow-outward currents, respectively, J_{fi} is the fast-inward current, and Θ represents the Heaviside function. The parameter values are listed in Table I.

B. Simulation details

We perform direct numerical simulations of the FK PDE model in a 2D homogeneous domain of size $N \times N$ with the no-flux boundary conditions. We employ a five-point stencil algorithm to solve the Laplacian and the forward Euler method for the time advancement. We use $N = 180$ with a spatial discretization of $\Delta x = 0.025$ cm and a time step of $\Delta t = 0.1$ ms, which, together with a diffusion coefficient $D = 0.0005$ cm^2/ms , satisfies the von Neumann stability criterion.

We track spiral wave tips every 10 ms using a standard method that computes the phase at each instant of time and each grid point [36]. By evaluating the line integral of the phase change around each grid point, we can identify a phase singularity (PS), which corresponds to the tip of a spiral wave. In this study, we vary the time constant τ_{-w} , which parametrizes the recovery duration of w , the plateau current J_{si} , and hence the action potential duration (APD) of u . It therefore determines the recovery time of an excitation, thereby controlling the ability of a tissue region to become excited again.

As our study is focused on SDC and intermittency, the different initial conditions for SDC were generated by starting with a dynamical state exhibiting multiple spiral waves and creating independent samples by adding uniformly distributed noise with an amplitude 10^{-5} to all three variables and at every grid point. These samples are then further evolved for a duration of 1 s to remove transient behavior, thereby finally creating multiple independent initial conditions. This procedure is repeated for each value of τ_{-w} considered and simulations continue until all activity is terminated. Since the termination time varies for different values of τ_{-w} (see below), the number of independent simulations ranges from 500 for $\tau_{-w} = 50 - 185$ ms to 246 for $\tau_{-w} = 200$ ms, 49 for $\tau_{-w} = 275$, 7 for $\tau_{-w} = 215, 250$ ms, and 8 for $\tau_{-w} = 300$.

III. RESULTS

A. SDC with intermittency

For small values of $\tau_{-w} < 150$ ms, the tissue recovers rapidly and a spiral wave becomes unstable close to its tip. As detailed in previous studies, this instability is due to a steep action potential duration restitution curve, which quantifies how the action potential duration depends on the previous action potential duration and the time between excitations [23,37]. As a result, the model exhibits SDC and the number of spiral wave tips, N_{PS} , fluctuates around an average number. Due to these fluctuations, the number of tips eventually reaches zero and SDC terminates. This is shown in Fig. 1(a), where we plot N_{PS} as a function of time, rescaled by the dominant period in the power spectrum, computed as $T_D = 80$ ms. This dominant period corresponds to the average period of a spiral wave in the SDC regime and is found to be largely independent of τ_{-w} . The insets show typical snapshots of the simulation, displaying the membrane potential using a color scale with red (blue) corresponding to high (low) values of u . These snapshots reveal unorganized dynamics and spiral waves that are continuously created and annihilated.

For increasing values of $\tau_{-w} \geq 150$ ms, the instability of spiral waves no longer occurs close to the tip as the restitution

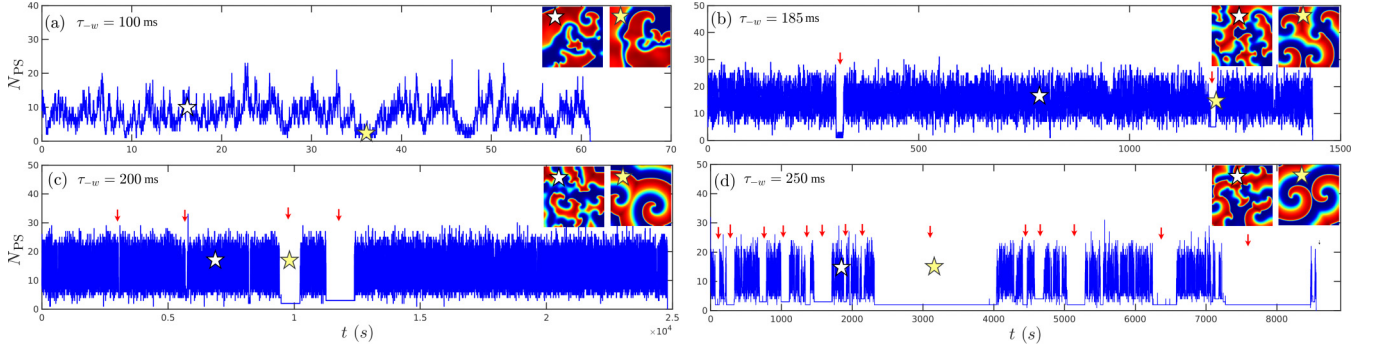


FIG. 1. The number of phase singularities N_{PS} as function of time for different values of τ_w . (a) Continuous SDC behavior marked by stochastic fluctuations in N_{PS} and an abrupt termination ($\tau_w = 100$ ms). (b)–(d) SDC intervals, intermittently interrupted by non-SDC intervals (indicated by red arrows) during which N_{PS} remains stable. The length of these non-SDC intervals grows with τ_w .

curve becomes flatter. Instead, the instability is characterized by far-field breakup, which occurs far from the spiral wave tip [23]. For these values of τ_w we find that the dynamics of the system changes: instead of exhibiting continuous SDC, the disordered state is intermittently interrupted by a dynamical state characterized by a small and stable number of spiral waves [Figs. 1(b)–1(d)]. This non-SDC state is also demonstrated in the accompanying snapshots of u , which show a small number of spiral waves with a much larger spatial extent than the spiral waves during the SDC interval. As the parameter is increased, the duration of these stable periods, indicated by red arrows, becomes longer until only a single spiral wave persists. In our study, simulations with $\tau_w = 300$ ms still exhibited periods of SDC, whereas all simulations with $\tau_w \geq 330$ ms eventually resulted in a single stable spiral wave. Thus, by varying a single parameter, the system's dynamics transition from completely disordered (SDC), to intermittently disordered, and finally to a fully ordered state.

The intermittent dynamics is further exemplified in Fig. 2, which shows three non-SDC intervals, again indicated by red arrows, sandwiched between SDC intervals. The lower panel shows, for the same time interval, the distance of the spiral wave tips to the lower left hand corner of the computational box, r . The first non-SDC interval contains a stable number of spiral waves (three) that are present for a duration of approximately $3000 T_D$. In both the second, much shorter-lived

non-SDC interval, and in the third non-SDC interval, lasting about $7000 T_D$, four spiral waves are present.

To quantify the extent of intermittency, we calculate the fraction of time the system spends in the non-SDC state. For this, we define a non-SDC interval as any interval of length greater than 1.5 s, corresponding to at least 19 rotations, in which the number of spiral wave tips remain stable. Next, we identify all pairs of successive non-SDC and SDC intervals and determine their respective duration, $t_{\text{non-SDC},i}$ and $t_{\text{SDC},i}$. For each pair i we calculate the fraction of time spent in the non-SDC state as $f_i = (t_{\text{non-SDC},i}) / (t_{\text{non-SDC},i} + t_{\text{SDC},i})$. We define the intermittency parameter, f , as the average of these individual fractions across all such pairs:

$$f = \frac{1}{n} \sum_{i=1}^n f_i, \quad (8)$$

where n is the total number of non-SDC/SDC pairs. Thus, $f = 0$ corresponds to continuous SDC behavior with no

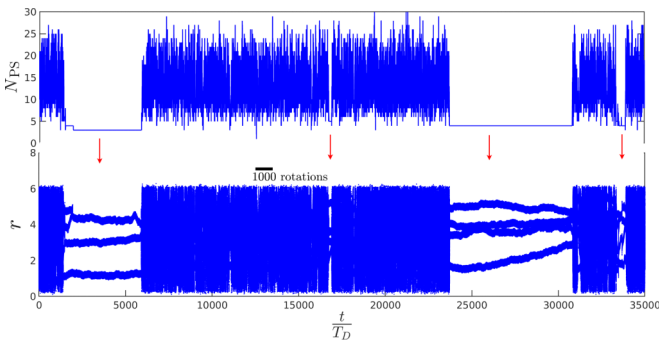


FIG. 2. Number of phase singularities (upper panel) and distance of spiral wave tips (lower panel) as a function of time ($\tau_w = 200$ ms), highlighting the stability of spiral waves during the non-SDC intervals (indicated by red arrows).

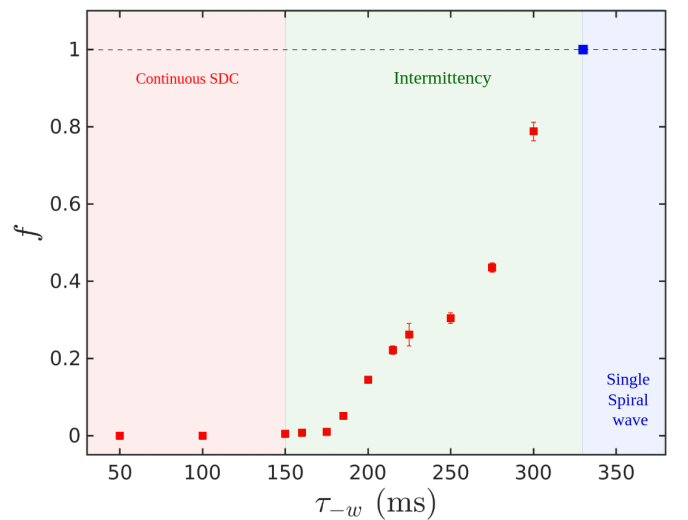


FIG. 3. Intermittency parameter f as a function of τ_w (red symbols) together with a blue symbol, representing the first parameter value for which all simulations resulted in a single spiral wave. The error bars are calculated using a bootstrap method with 10 000 resamples. The different dynamical regimes of the model are color coded.

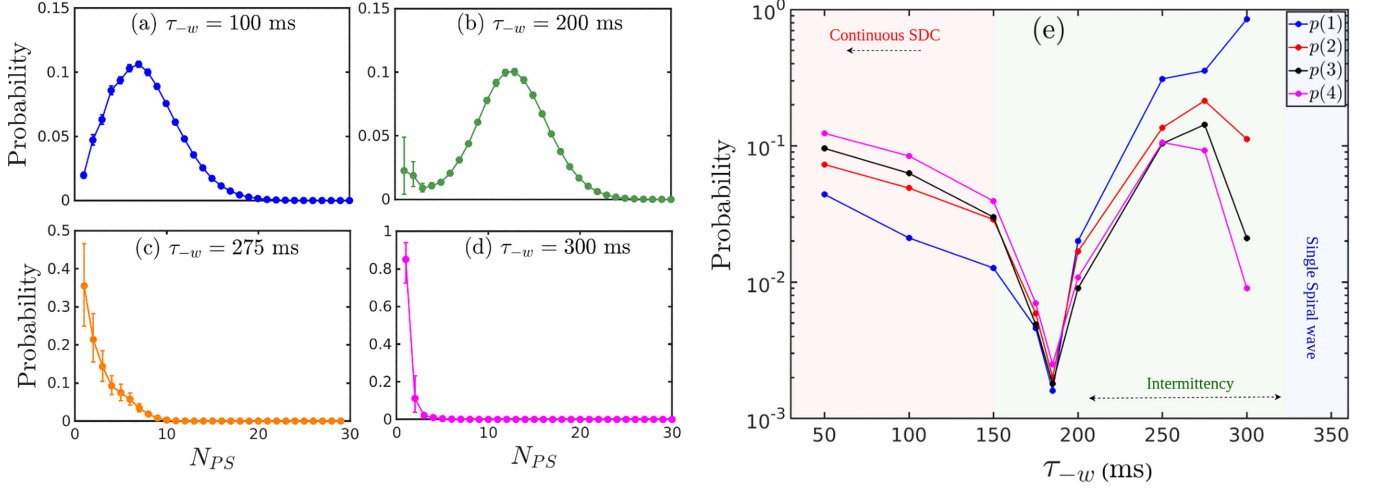


FIG. 4. (a)–(d) Probability distribution of N_{PS} for different values of τ_{-w} . Error bars represent standard deviations and solid lines correspond to mean values. (e) Probability of the system residing at $N_{PS} = 1, 2, 3$, and 4 for different values of τ_{-w} .

intermittency and $f = 1$ corresponds to a state with a spiral wave. In Fig. 3 we plot f as a function of τ_{-w} as symbols. Consistent with Fig. 1, we can identify three regions in this plot: a region corresponding to continuous SDC (pink region), a region corresponding to intermittency (green region), and a region corresponding to a single spiral wave (blue region). Clearly, within the intermittency region, the fraction of time spent in the non-SDC state gets larger as τ_{-w} increases.

B. Distribution of spiral wave tips

To further quantify the intermittency, we compute the probability distribution of spiral wave tips for different values of τ_{-w} (Fig. 4). For values corresponding to continuous SDC [Fig. 4(a)], the distribution displays the characteristic bell-shaped curve discussed in previous work with the probability smoothly decreasing as the number of tips approaches one [27]. In this case, the mean termination time is proportional to the inverse of the probability of having a single spiral tip in the domain [$p(N_{PS} = 1)$] such that it decreases for increasing values of this probability [27]. For increasing values of τ_{-w} in the intermittency region, however, the distribution starts to exhibit a "bump" for small values of N_{PS} , reflecting the non-SDC intervals with a several quasistable (since they eventually destabilize) spiral waves [Fig. 4(b)]. For even larger values of τ_{-w} the distribution is dominated by small values of N_{PS} [Figs. 4(c) and 4(d)], indicating that the dynamics is mainly governed by non-SDC intervals. Furthermore, since for large values of τ_{-w} a single spiral wave is stable, the distribution for $\tau_{-w} = 300$ ms becomes highly peaked at $N_{PS} = 1$ [see Fig. 4(d)].

The increase in the probability of having a small number of tips is also shown in Fig. 4(e) where we plot $p(N_{PS})$ for $N_{PS} = 1 - 4$ as a function of τ_{-w} . These probabilities decrease for values of τ_{-w} up to $\tau_{-w} = 185$ ms. This decrease becomes more pronounced when the intermittency regime is entered. For $\tau_{-w} > 185$ ms, the probabilities increase, reflecting the dominance of non-SDC intervals. Note that for large values of τ_{-w} , but before entering the regime of a single spiral

wave, $p(N_{PS} = 1)$ continues to increase at the expense of $p(N_{PS} \neq 1)$.

C. SDC with intermittency increases the mean termination time

The appearance of intermittent non-SDC intervals implies that the mean termination time can no longer be approximated using $p(N_{PS} = 1)$. Instead, these non-SDC intervals, containing a few spiral wave tips, will increase the mean termination time. To quantify this increase and the dependence of T_{term} on τ_{-w} , we compute the termination time of a large number of simulations (> 100) each initialized with independent initial conditions. Examples of the resulting distribution of termination times are presented in Fig. 5 for a value of τ_{-w} in the continuous SDC regime (a) and for values in the intermittent regime (b)–(d). In the continuous SDC regime, the distribution is exponential, consistent with previous work [27,28], as can also be seen by the exponential fit [dashed line in Fig. 5(a)]. In the intermittent regime, however, the termination times exhibit a long-tailed distribution, corresponding to simulations with multiple or long-lasting non-SDC intervals.

Using these termination times, we compute the mean termination time as a function of τ_{-w} [solid circles Fig. 5(e)]. In the continuous SDC regime, we find that T_{term} increases linearly with τ_{-w} . Once τ_{-w} enters the intermittent regime, however, T_{term} becomes strongly nonlinear and sharply increases by almost three orders of magnitude between $\tau_{-w} = 150$ ms and $\tau_{-w} = 200$ ms. Note that due to the computational expense, we are not able to compute T_{term} for larger values of τ_{-w} . Also note that for $\tau_{-w} \geq 330$ ms only a single spiral wave exists, implying $\tau \rightarrow \infty$.

For values of τ_{-w} in the intermittency regime, we also compute the average amount of time spent in the SDC state before termination, T_{SDC} [open red stars in Fig. 5(e)]. For values up to $\tau_{-w} = 175$ ms, this time is almost indistinguishable from T_{term} , indicating that the non-SDC intervals are not significantly affecting the mean termination time. Of course, this is consistent with the small value of f for these choices of τ_{-w} (Fig. 3). In other words, the sharp increase in T_{term} is not due to the system spending more time in the non-SDC state.

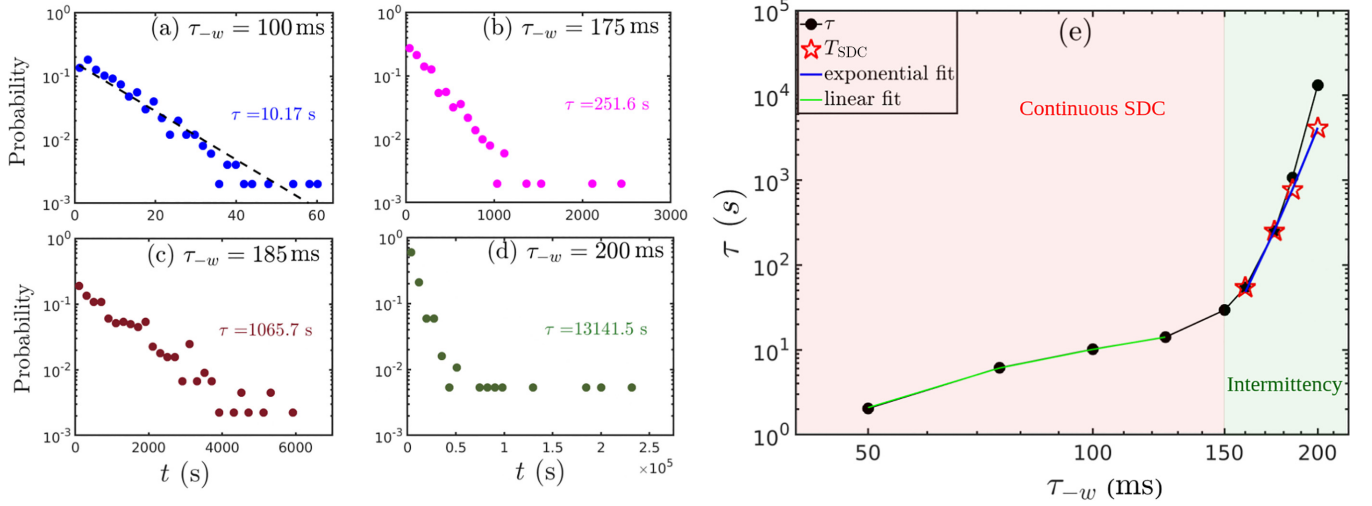


FIG. 5. (a)–(d) Semilogarithmic plot of the probability distribution of termination times for increasing values of τ_{-w} . The dashed line in (a) represents an exponential fit. (e) T_{term} as a function of τ_{-w} (solid symbols) and the time spent in the SDC state (open symbols). In the continuous SDC parameter regime, the increase in τ is linear, as shown by the linear fit (green line). In the intermittency parameter regime, the time spent in the SDC state (τ_{SDC} , red stars) increases exponentially as demonstrated by the exponential fit (blue line). Notice the growing difference between T_{SDC} (red stars) and T_{term} (black filled circles) for increasing values of τ_{-w} , implying that non-SDC regions exert substantial influence on the mean termination time.

Instead, it is due to the significant reduction in the probability of having a small number of tips, as shown in Fig. 4(e).

The correlation between the appearance of intermittent non-SDC intervals and the termination time T_{term} can be further illustrated by examining multiple terminating simulations. For this, we compute the number of intermittent non-SDC intervals, n_S , for each separate terminating simulation. As shown in Figs. 6(a) and (b) for two different values of τ_{-w} , n_S exhibits a clear positive correlation with T_{term} . Thus, for a fixed value of τ_{-w} , simulations with more intermittent intervals tend to terminate later.

To further verify that the presence of quasi-stable spirals increases T_{term} , we calculate the lifetime of each spiral wave tip, t_{PS} . The probability distribution of these lifetimes is presented in Fig. 6(c) for different values of τ_{-w} . For small values of τ_{-w} that correspond to continuous SDC (red symbols), the lifetimes are at most several seconds. As τ_{-w} increases, however, the probability distribution shifts to larger values of t_{PS} due to the appearance of long-lasting, quasistable spiral

waves. For example, for $\tau_{-w} = 200$ ms spiral waves can last for more than 10^3 s, leading to large termination times.

Finally, we want to point out that it is also possible to have intermittently present quasistable spiral waves in part of the computational domain while the remainder of the domain exhibit SDC. This is illustrated in Fig. 7 where we plot N_{PS} (upper panel) and r as a function of normalized time. While N_{PS} fluctuates during this time interval, r for some spiral waves clearly remains constant, as indicated by the dashed red lines. In other words, quasistable spiral waves coexist with stochastically formed spiral waves, and these waves were not considered when computing f (Fig. 3), nor in determining the data presented in Fig. 6(a) and (b). Examining our simulation results reveals that this co-existence becomes more prominent for $\tau_{-w} \geq 200$ ms.

IV. CONCLUDING REMARKS

In this paper, we show that cardiac models can exhibit intermittent dynamics during which periods of SDC are

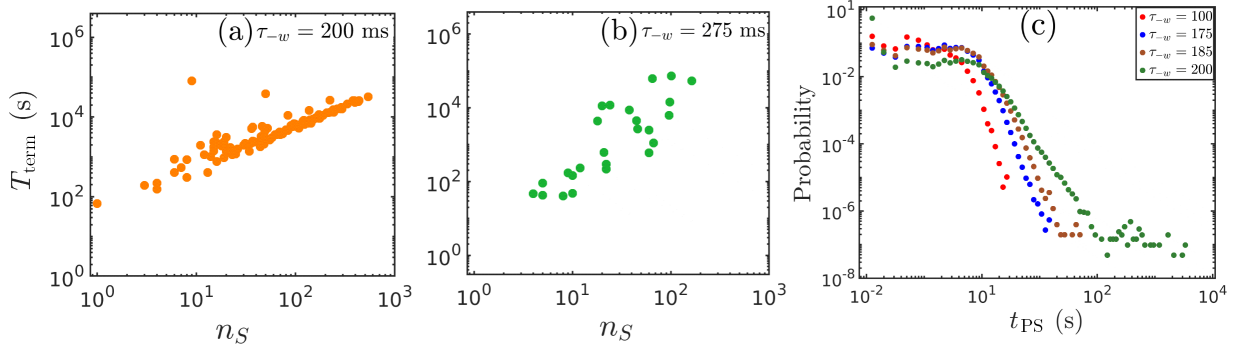


FIG. 6. (a), (b) Mean termination time as a function of the number of non-SDC intervals for $\tau_{-w} = 200$ ms (a) and $\tau_{-w} = 275$ ms (b). Each symbol represents a simulation in which SDC terminates. (c) Probability distribution of spiral wave lifetimes for different values of τ_{-w} . As τ_{-w} increases, longer lives spiral waves become more common.

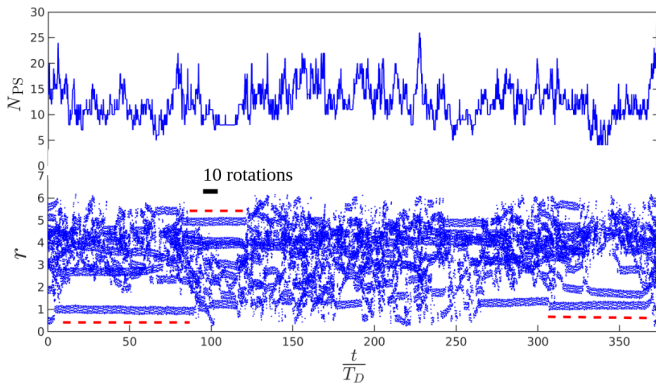


FIG. 7. Number of spiral wave tips (upper panel) and distance of tips to corner of computational domain (lower panel) as a function of normalized time ($\tau_{-w} = 200$ ms). Quasistable spiral waves that coexist with SDC are indicated by dashed red lines.

alternated with periods of a more ordered dynamical state, characterized by a small number of quasistable spiral waves. This intermittency manifests itself when we vary a single parameter, τ_{-w} in the FK model, representing the recovery time duration of one of the model variables. In fact, by varying this parameter across a range of values, we show that the system transitions from SDC to intermittent dynamics, and ultimately to a single spiral wave. The dynamics can be quantified using an intermittency parameter f , which measures the fraction of time the system was in the more ordered, non-SDC state. This parameter shows a transition from 0, representing continuous SDC, to 1, corresponding to a single spiral wave, over a limited range of τ_{-w} . As a result of the appearance of the intermittent, non-SDC intervals, the mean termination time of wave activity increases dramatically, especially for values of τ_{-w} that approach the regime of a single spiral wave. Thus, similar to changing the area of the computational domain, altering this parameter can significantly lengthen the mean termination time. We should comment here that the intermittent behavior is not restricted to the particular parameter change, parameter set, or model under consideration. We have observed similar behavior when changing another parameter (τ_{+w}), using other parameter sets of the FK model, and in a generic two-variable model [38].

The fact that the termination time sharply increases as τ_{-w} increases and enters the intermittency regime is perhaps not unexpected. After all, for small values of τ_{-w} , the system exhibits SDC, which has a finite lifetime [see Fig. 5(e)]. On the other hand, for large values of τ_{-w} , the system becomes ordered and exhibits a single spiral wave with a termination

time that becomes infinite. In the range of parameter values between these two extremes, the termination time increases rapidly due to the appearance of longer and longer non-SDC intervals (see Fig. 6).

Intermittency is a fundamental phenomenon in dynamical systems where the system alternates between periods of regular behavior and bursts of chaotic or disordered activity. It was first described in dissipative systems, where it was shown to be a key route to chaos [39]. Intermittent dynamics can be found in biological and biochemical systems [40–42] and is wide spread in physical systems. It has been particularly well studied in fluid dynamics, where varying the Reynolds number can cause a transition from laminar flow to intermittent and ultimately fully turbulent behavior [43,44]. Thus, our control parameter, τ_{-w} , plays a role analogous to the Reynolds number in fluid flow, with laminar flow corresponding to a single spiral wave and turbulent behavior corresponding to SDC. However, contrary to fluid flow, SDC can terminate, resulting in the complete cessation of all activity.

The observed intermittency may have clinical relevance for AFib. In many patients, AFib is initially intermittent with periods of fibrillation alternating with periods of normal sinus rhythm. While our simulations reveal an alternation between SDC—believed to underlie AFib—and more organized non-SDC states, it is possible that, in the presence of periodic pacing, as occurs in the real heart, the non-SDC state becomes even more organized. This increased organization may eventually lead to a transition into sinus rhythm. Investigating such a scenario would require simulating SDC and its intermittency using realistic cardiac geometries that include periodic pacing from the sinoatrial node. In future work, we plan to address this problem. In addition to this extension, we also plan to extend our intermittency study to other cardiac models, including more detailed ones. This will allow us to determine whether specific ion channels contribute to the emergence of intermittency, possibly identifying therapeutic targets that can shorten the duration of AFib in patients.

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DATA AVAILABILITY

The data that support the findings of this article are openly available [45].

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