

Strings, Branes and Twistons: Topological Analysis of Phase Defects in Excitable Media Such as the Heart

Louise Arno^{1,*}, Desmond Kabus^{1,2,*} and Hans Dierckx^{1,2,†}

¹Department of Mathematics, *KU Leuven Campus Kortrijk, Kortrijk, Belgium*

²Department of Cardiology, *Leiden University Medical Center, Leiden, The Netherlands*



(Received 21 March 2025; accepted 17 July 2025; published 18 September 2025)

Several excitable systems, such as the heart, self-organize into complex spatiotemporal patterns that involve wave collisions and rotating vortices. The dynamics between these structures are incompletely understood. Here we establish a comprehensive topological framework in three spatial dimensions. Conduction blocks are identified as phase defect surfaces, on which three types of closed curves move and carry a topological vector charge. Our framework not only sheds new light on twistons and hybrid reentry but also predicts new states: a Möbius scroll wave and conduction block surfaces that can split, branch, or contain multiple filaments. We hypothesize that the latter play a role in cardiac arrhythmias.

DOI: [10.1103/5pgp-1wj6](https://doi.org/10.1103/5pgp-1wj6)

Introduction—Several interesting natural systems gain their complex dynamics from the interaction between coupled excitable elements [1–3]. In these systems, the spatiotemporal pattern emerges from self-organization and tends to determine the global state of the system. In cardiac tissue, the precise mechanisms sustaining complex arrhythmias are incompletely understood [4,5].

It was found that excitable systems can be better understood by studying self-emerging dynamical structures that arise in them. These structures include traveling wave fronts, where elements become excited, and wave backs, where elements return to the resting state. In the classical picture and two spatial dimensions (2D), the wave front and wave back touch in a phase singularity (PS) [6–8]. These PSs form a rotor filament in three spatial dimensions (3D) [7–9]. However, the concept of rotor filaments has some shortcomings. In experiments, the scroll waves of activation that rotate around the filaments are often short lived, lasting seldom longer than a rotation. Furthermore, simultaneous recordings on the inner and outer surface of the heart can reveal a markedly different activation pattern on either surface [10]. Also, the PSs seen on the cardiac surface were found to colocalize with sites of the conduction block, i.e., where a wave front hits unrecovered tissue [11–13]. Ablating rotor cores was suggested as a way to stop ventricular arrhythmias [14], but more recently

regions of increased spatiotemporal dispersion are being targeted [15].

In this Letter we elucidate how excitation structures in 3D media topologically relate to each other, encompassing concepts as long- and short-lived rotors [14], conduction blocks [16,17], wavelets [18], and twistons [19].

Elements from 2D theory—We build further on the recent 2D theory that recognized wave blocks and linear cores as phase defects (PDs) [12,13,20,21]. We provide a summary here and details in Appendix A. The central idea is to divide the state space of the excitable systems into excited, unexcited, and physiologically forbidden parts; see Fig. 1(a). When this partition is mapped to physical space, the forbidden zone becomes a phase defect, while boundaries between excited and unexcited regions become the wave front and back. Every wave front has two end points, with orientation, which were called heads $h^\pm$ with positive or negative charge Q depending on chirality [see Eq. (A1)]. Similarly, we defined the end points of wave backs as tails, $t^\pm$. The end points of the typically elongated phase defects correspond to well-known turning points of a spiral tip trajectory, which we called pivot particles $p_\pm$, for which we defined a topological charge P ; see Eq. (A3) [20].

Theoretical framework in 3D—Figures 1(c) and 1(d) show 3D simulations in the Bueno-Orovio-Cherry-Fenton (BOCF) cardiac monodomain model [22,25]. Just like a PS extends to filament curves [8,9,26–28], heads, tails, and pivots become curves in 3D; see Figs. 1(c)–1(f). Since all wave fronts are surfaces, the head curves must form closed loops. Because wave fronts are oriented, a head curve can be assigned continuous vector charge $\vec{H}$; see the arrow in Figs. 1(e) and 1(f). When pointing your right-hand thumb in the direction of wave propagation, your other fingers indicate the sense of $\vec{H}$. $\vec{H}$ is related to the 2D head charge;

*These authors contributed equally to this work.

†Contact author: h.j.f.dierckx@lumc.nl

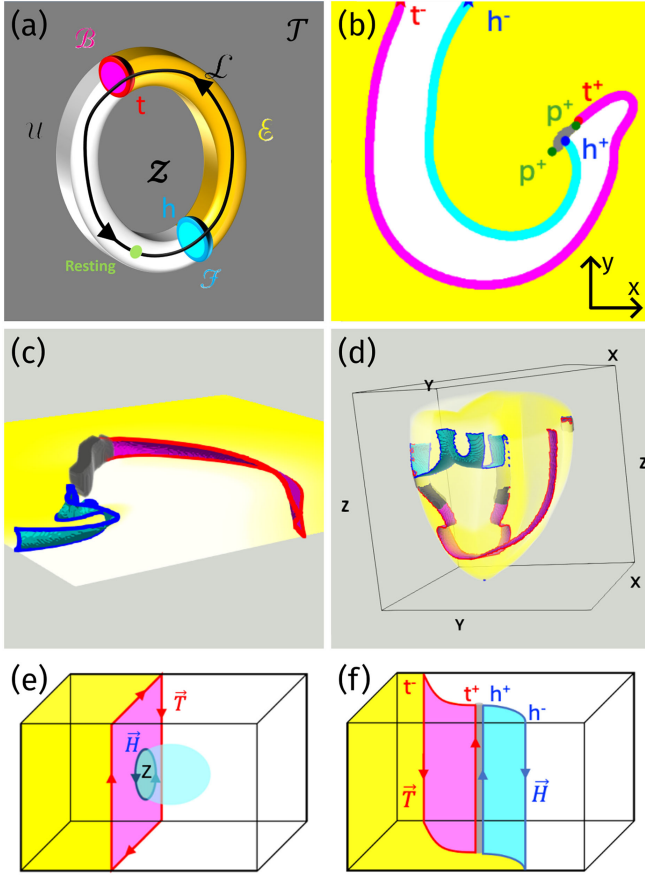


FIG. 1. (a) Torus-shaped attractor in state space, surrounded by a physiologically “forbidden” zone (gray). (b) Linear-core spiral in the FK model [19], showing the excited region (yellow), phase defect (gray), wave front (cyan), wave back (magenta), heads (blue), tails (red) and pivots (green) [20]. (c) 3D linear-core scroll wave [22] rotating around a phase defect surface (PDS). (d) PDSs in a 3D biventricular geometry [23], see also Supplemental Movie [24]. (e) Creation of a closed head loop around a PDS when a stimulus is given near a wave back. (f) A straight scroll wave exhibiting closed head and tail curves that run parallel at the filament.

see Fig. 1(f): if only the top surface is seen (as in cardiac surface recordings), the upward pointing $\vec{H}$ reaching the surface manifests as a h^+ particle, while the downward pointing $\vec{H}$ produces a h^- . The wave front on a boundary surface of the medium carries $\vec{H}$ charge, pointing from h^+ to h^- .

Likewise, tail curves in 3D must also form closed loops. The sense of the vectorial tail charge $\vec{T}$ is given by the fingers of your right hand if your thumb points towards the excited region. Figure 1(f) depicts a straight scroll wave rotating around a classical rotor filament. The filament is found as a region where a head and tail curve run parallel to each other in the same direction. When meeting the medium boundary, the head and tail each return along a different path to the other side, forming closed loops.

The classical $Q = 1$ gets distributed over a head and a tail curve, each carrying $Q = 1/2$.

The topological charge of heads and tails is inherited in 3D directly from Eq. (A1). Already known from classical theory [8], any closed contour in the medium on which ϕ is defined everywhere will deliver the same integer result Q if the contour is continuously shifted or deformed. Here, we note that the intersection between phase defect (Z) and excited (E) and unexcited (U) regions must be a continuous, oriented curve; hence it follows that the $\vec{H}$ and $\vec{T}$ are preserved along the head and tail curves.

Next, we turn to pivots. In 3D, PD lines become extended phase defect surfaces (PDSs); see [13] and Figs. 1(c)–1(e). If the conduction block manifests as a surface in 3D, it has a well-defined rim, around which the excitation suddenly changes direction. Figure 2 shows examples of such pivot curves. Figure 2(a) shows a local wave block inside the medium: a propagating wave from the front of the medium to the back reaches an refractory region and needs to travel around it, as indicated by the double arrows. The rim of the PDS is a pivot curve

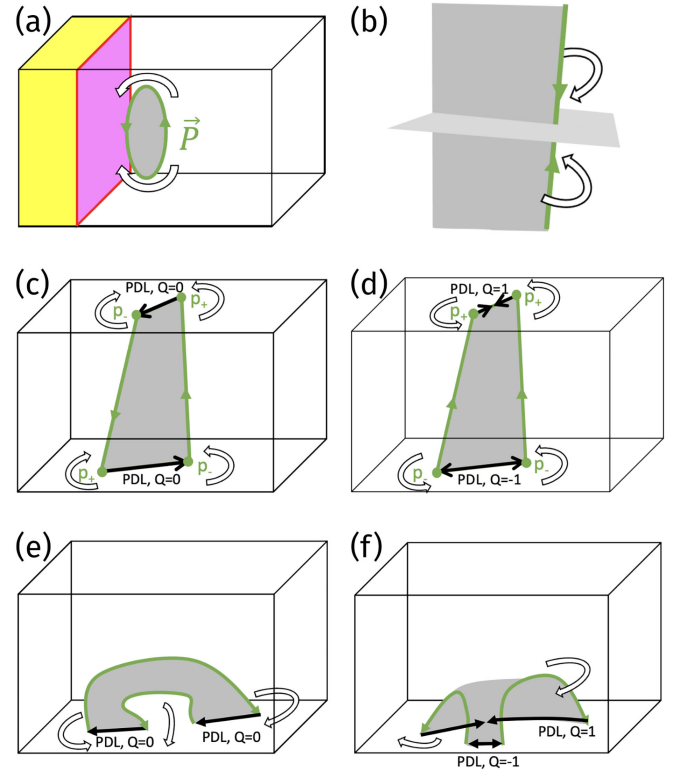


FIG. 2. Pivot curves (green) at the rim of a PDS in 3D. Double arrows indicate scroll wave motion. (a) Situation of Fig. 1(e), later in time. (b) Argument why the direction of the $\vec{P}$ cannot suddenly change along a pivot curve. (c) A PDS with antiparallel pivot curves indicates a conduction block. (d) A PDS with parallel pivot curves marks a linear rotor core. (e) U-shaped PDS representing a conduction block (not reentry). (f) U-shaped PDS that forms an isthmus for reentry.

(in green), to which we associate a direction using the right-hand rule: if your fingers curl like the wave turning around the pivot, your thumb indicates the direction of the pivot curve's vector charge $\vec{P}$. Figure 2(b) demonstrates why a pivot field $\vec{P}$ cannot suddenly change direction along a pivot curve. Consider the dark gray PDS. If the sense of its pivot curve were to change direction, there would be a scroll wave that changes spatially its rotation direction when moving along the pivot curve. Then, the phases of the excitable elements will not be continuous, and there must be another PDS (light gray) that intersects the first PDS. Thus, pivot curves have a continuous vector charge, but PD surfaces may intersect; see below.

When the wave block from Fig. 2(a) grows and collides with the medium boundaries, a transmural conduction block can form [Fig. 2(c)]. The direction of rotation shows that $\vec{P}$ runs along both sides in opposite sense. At the top and bottom surfaces, the pivot curve ends in a p_+ , i.e., a pivot point where the wave rotates half a turn to the left, seen from outside the medium. Likewise, it emerges from p_- points on the medium boundary. We can make the pivot curves continuous by assigning a $\vec{P}$ -charge to a PD line with $Q = 0$ on the medium surface, flowing from p_+ to p_- . The case of a linear-core scroll wave is different; see Fig. 2(d). Here, the wave turns around both pivot lines in the same direction, and on the outer medium boundary, PD lines of topological charge $P = Q = \pm 1$ are seen. In the case drawn, one has two p_- on the bottom medium boundary and two p_+ on the upper medium boundary. Here too, the $\vec{P}$ is directed in the bulk from p_- to p_+ . Thus, the PD lines from 2D theory [12,13] are a net source of $\vec{P}$ in 3D. We added the following $\vec{P}$ charge arrows to the figures for clarity: $p_- \leftrightarrow p_-$, $p_+ \rightarrow \leftarrow p_+$, and $p_+ \rightarrow p_-$. This way, we obtain a visual language to reason about conduction blocks. Figure 2(e) shows a PDS, and Fig. 2(f) depicts propagation through an isthmus, a typical situation during ventricular tachycardia.

Applications of the theoretical framework—With the above framework, we are able to unravel the nature of previously observed emerging phenomena and predict the existence of new structures. Fenton and Karma reported that if a linear-core scroll wave is initiated in a medium with locally varying myofiber orientation, the rotor filament exhibits local concentrations of twist which travel along the filament [19]. Figure 3(a) clarifies the nature of this “twiston”: the classical filament colocalizes with the head curve in our theory, which travels around the PDS. Due to anisotropic wave propagation, not all points of the head curve reach the pivot curve simultaneously. So, during the rotation, there is an intersection point between the head curve and the pivot, which can travel at arbitrary speed along the pivot curve. We thus identify Fenton’s twiston as a “cardion” of codimension 3.

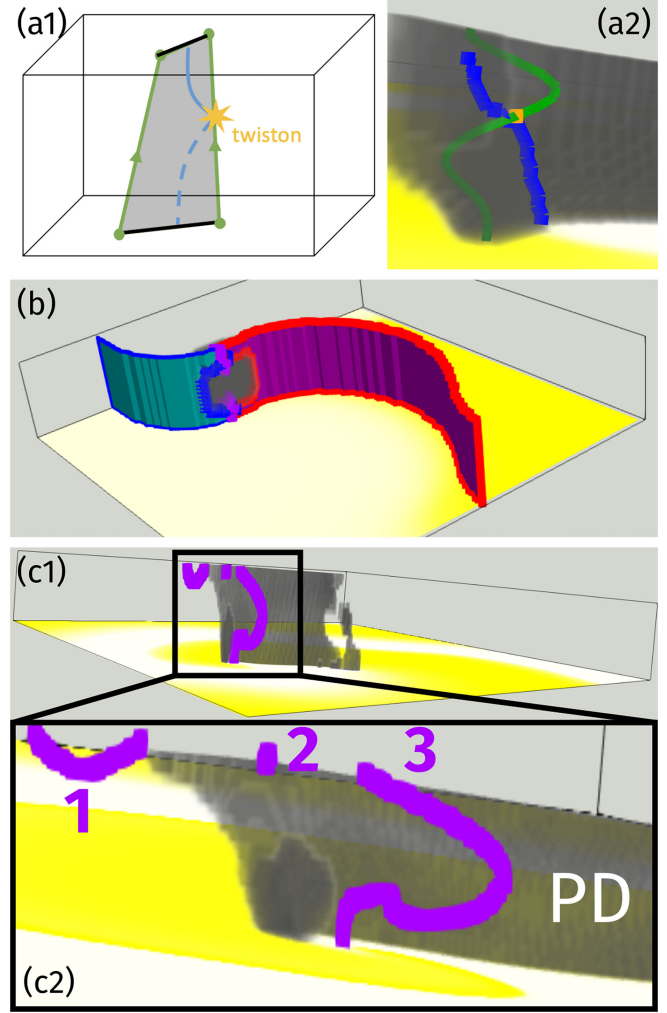


FIG. 3. Fitting of observed structures into the framework. (a) Fenton’s twiston as the intersection of a head and pivot curve, as a concept (a1) and in simulation (a2). (b) In hybrid reentry around an obstacle, the filament is split into a head and tail curve on the obstacle’s surface. (c) Multiple classical filaments on the same conduction block surface.

Second, our framework can deal with how conduction blocks and rotors interact with obstacles. Figure 3(b) shows a circular rotor intersecting an unexcitable obstacle. Since real excitable media such as cardiac tissue include a lot of

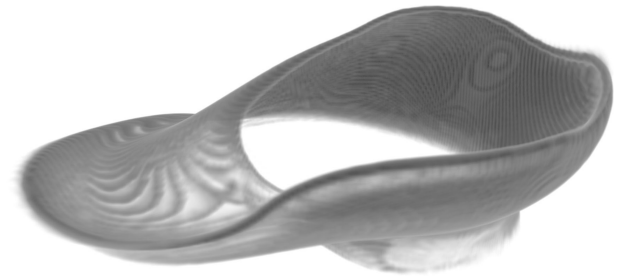


FIG. 4. Numerical simulation featuring a phase defect surface shaped as a Möbius strip. See Supplemental Movie [24].

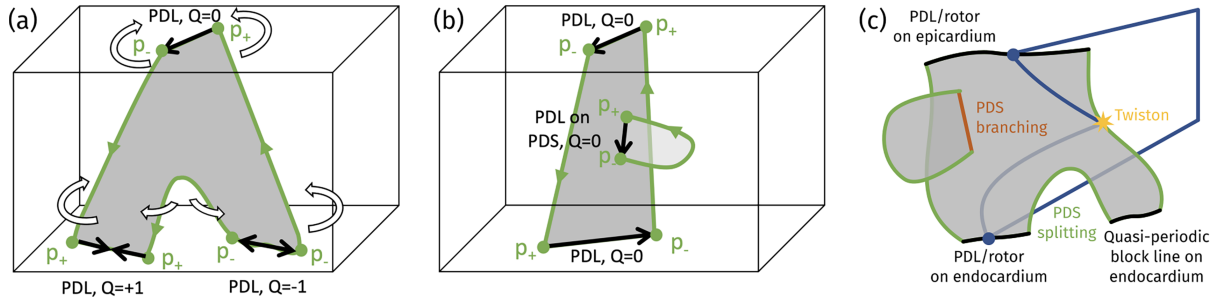


FIG. 5. Complex excitation structures predicted and explained by the framework. (a) Λ -shaped conduction block surface (PDS). (b) Conduction block surface with a side branch (PDS). (c) Sketch of an excitation structure that may underly complex surface activation: a branching, splitting PDS, around which head and tail curves revolve.

inhomogeneities, most reentrant patterns may be of this hybrid type. While the filament (purple) is interrupted at the obstacle, head and tail curves are always closed.

Third, we found that multiple head curves may travel around the same PDS. Figure 3(c) shows a simulation example. The classical filament picture misses how the filaments are connected by a conduction block.

Now, we describe several novel phenomena in excitable media predicted by our framework. Since a PDS does not need to be an orientable surface, we managed to numerically simulate a scroll wave rotation around a PDS that is shaped as a Möbius strip; see Fig. 4. Hereto, we sampled frames from half a rotation of a linear-core spiral wave in a 2D BOCF model, isotropic medium, and pasted them along a circle in toroidal coordinates in 3D while rotating the solution over 180° when the circle was traversed. As a result, we find a scroll ring that looks untwisted at a large distance but whose head curve crosses the rim of the strip twice, yielding two twistons. The edge of the strip is one continuous pivot curve without changes in the direction of the pivot field. The rotation of the scroll wave was stable for at least ten rotations.

While the classical theory only has U, I, and O-shaped filaments, conduction block surfaces can take infinitely many more topological shapes. Figure 5(a) illustrates a PDS splitting with a Λ -shaped conduction block. There are several possible rotation senses of a scroll wave around it, which can be made consistent by using the $\vec{P}$ -charge direction. Note that arbitrarily complex patterns (W, X, ...) are admitted, and we expect these to happen in the heart when markedly different patterns are observed on the epi- vs endocardial surfaces. Figure 5(b) illustrates that PDSs can have side branches. Suppose a linear-core rotor, connecting top and bottom surfaces, exists. If a region in the middle requires a slightly longer time for recovery, a PDS can form as a side branch of the first PDS. Where the second PDS attaches to the first one, a PD line is found on the initial PDS.

In real 3D media, the three flavors of closed curves are present at the same time and bound to the same PDs.

Figure 5(c) sketches a complex branching PDS combining many of the nontrivialities above. In a heterogenous or anisotropic medium, we expect such complex PDS shapes, on which the head curve (detected as a classical filament) rotates. In Fig. 5(c), every rotation of the head curve around the PDS requires the head curve to also circle both “feet” of the PDS, such that the timing is correlated between both endocardial conduction block lines. This behavior is consistent with our experimental observation of ventricular tachycardia [13].

Discussion—This work complements other topological approaches [8,28–30] and aims to provide a unifying viewpoint on various structures in literature. We purposely designed a framework that can also handle obstacles, boundaries, and inhomogeneities. Based on Figs. 3–5, we suggest that extended PDSs may play a role in epi-endocardial dissociation, in addition to physical separation between the inner and outer layers [31]. We contribute topological constraints that patterns need to satisfy in 3D, extending the 2D quasiparticle framework [20]. We assumed a torus-shaped attractor that disregards certain memory effects [32–34], so more work is required to cover afterdepolarizations or alternans. We are preparing automated detection methods [35] and look forward to study how the identified structures interact, e.g., by calculating the mutual “forces” between them.

We find that excitable media contain conserved structures of given codimension, which end on higher-dimensional boundary surfaces and induce topological charge on them, which is somewhat reminiscent of D-brane theory [36].

Conclusion—A 3D description of complex excitable patterns was presented using three different types of closed curves that are attached to phase defect surfaces. These surfaces may split or branch to become arbitrarily complex and could be driving or sustaining several processes in excitable media.

Acknowledgments—We thank P. Claus, D. A. Pijnappels, T. De Coster, O. Bernus, H. Verschelde, A. V. Panfilov, J. Ector, and A. Gobeyn for helpful discussions and

remarks. L. Arno was funded by FWO-Flanders, Grant No. 117702N. D. K. was supported by KU Leuven Grant No. GPUL/20/012. H. D. was supported by ST/019/007 (KU Leuven) and the LUMC 2024 Fellowship. L. A. contributed to the numerical simulations, data analysis, scientific discussions, and writing of the manuscript. D. K. contributed to the numerical simulations, data analysis methods, scientific discussions, simulation software, and writing of the manuscript. H. D. contributed to the central idea of seeing the classical filament as a conduction block surface, simulation software, data analysis methods, scientific discussions, and writing of the manuscript. Correspondence and requests for materials should be addressed to H. D.

Data availability—The data that support the findings of this Letter are openly available [37,38].

- [1] *Cardiac Electrophysiology. From Cell to Bedside*, 2nd edition, edited by D. Zipes and J. Jalife (Saunders, Philadelphia, 1995).
- [2] K. M. Sanders, Spontaneous electrical activity and rhythmicity in gastrointestinal smooth muscles, in *Smooth Muscle Spontaneous Activity: Physiological and Pathological Modulation*, edited by H. Hashitani and R. J. Lang (Springer, Singapore, 2019), pp. 3–46.
- [3] J. V. Noble, Geographic and temporal development of plaques, *Nature (London)* **250**, 726 (1974).
- [4] M. Nash, A. Mourad, R. Clayton, P. Sutton, C. Bradley, M. Hayward, D. Paterson, and P. Taggart, Evidence for multiple mechanisms in human ventricular fibrillation, *Circulation* **114**, 536 (2006).
- [5] J. W. Waks, Mechanisms of atrial fibrillation—reentry, rotors and reality, *Arrhythm Electrophysiol. Rev.* **3**, 90 (2014).
- [6] V. Zykov, *Simulation of Wave Processes in Excitable Media* (Manchester University Press, Manchester, 1987).
- [7] R. Gray, J. Jalife, A. Panfilov, W. Baxter, C. Cabo, and A. Pertsov, Non-stationary vortex-like reentrant activity as a mechanism of polymorphic ventricular tachycardia in the isolated rabbit heart, *Circulation* **91**, 2454 (1995).
- [8] R. Clayton, E. Zhuchkova, and A. Panfilov, Phase singularities and filaments: Simplifying complexity in computational models of ventricular fibrillation, *Prog. Biophys. Molec. Biol.* **90**, 378 (2005).
- [9] A. Winfree, Scroll-shaped waves of chemical activity in three dimensions, *Science* **181**, 937 (1973).
- [10] M. Yamazaki, S. Mironov, C. Taravant, J. Brec, L. Vaquero, K. Bandaru, U. Avula, H. Honjo, I. Kodama, O. Berenfeld, and J. Kalifa, Heterogeneous atrial wall thickness and stretch promote scroll waves anchoring during atrial fibrillation, *Cardiovasc. Res.* **94**, 48 (2012).
- [11] P. Podziemski, S. Zeemering, P. Kuklik, A. van Hunnik, B. Maesen, J. Maessen, H. J. Crijns, S. Verheule, and U. Schotten, Rotors detected by phase analysis of filtered, epicardial atrial fibrillation electrograms colocalize with regions of conduction block, *Cir. Arrhythmia Electrophysiol.*, 10.1161/CIRCEP.117.005858 (2018).
- [12] N. Tomii, M. Yamazaki, T. Ashihara, K. Nakazawa, N. Shibata, H. Honjo, and I. Sakuma, Spatial phase discontinuity at the center of moving cardiac spiral waves, *Comp. Biol. Med.* **130** (2021).
- [13] L. Arno, J. Quan, N. Nguyen, M. Vanmarcke, E. G. Tolkacheva, and H. Dierckx, A phase defect framework for the analysis of cardiac arrhythmia patterns, *Front. Physiol.*, 10.3389/fphys.2021.690453 (2021).
- [14] S. M. Narayan, D. E. Krummen, K. Shivkumar, P. Clopton, W.-J. Rappel, and J. M. Miller, Treatment of atrial fibrillation by the ablation of localized sources, *J. Am. College Cardiol.* **60**, 628 (2012).
- [15] J. Seitz, C. Bars, G. Théodore, S. Beurtheret, N. Lellouche, M. Bremond, A. Ferracci, J. Faure, G. Penaranda, M. Yamazaki, U. M. R. Avula, L. Curel, S. Siame, O. Berenfeld, A. Pisapia, and J. Kalifa, AF ablation guided by spatiotemporal electrogram dispersion without pulmonary vein isolation, *J. Am. College Cardiol.* **69**, 303 (2017).
- [16] M. Janse, Vulnerability to ventricular fibrillation, *Chaos* **8**, 149 (1998).
- [17] J. Jalife, Ventricular fibrillation: Mechanisms of initiation and maintenance, *Annu. Rev. Physiol.* **62**, 25 (2000).
- [18] G. Moe and J. Abildskov, Atrial fibrillation as a self-sustained arrhythmia independent of focal discharge, *Am. Heart J.* **58**, 59 (1959).
- [19] F. Fenton and A. Karma, Vortex dynamics in three-dimensional continuous myocardium with fiber rotation: Filament instability and fibrillation, *Chaos* **8**, 20 (1998).
- [20] L. Arno, D. Kabus, and H. Dierckx, Analysis of cardiac arrhythmia sources using Feynman-like diagrams, *Sci. Rep.* **14**, 28962 (2024).
- [21] D. Kabus, L. Arno, L. Leenknecht, A. Panfilov, D. Pijnappels, and H. Dierckx, Numerical methods for the detection of phase defect structures in excitable media, *PLoS One* **17**, e0271351 (2021).
- [22] A. Bueno-Orovio, E. Cherry, and F. Fenton, Minimal model for human ventricular action potentials in tissue, *J. Theor. Biol.* **253**, 544 (2008).
- [23] R. Hren and G. Strohink, Application of surface harmonic expansions for modeling human torso, *IEEE Trans. Biomed. Eng.* **42**, 521 (1995).
- [24] See Supplemental Material at <http://link.aps.org/supplemental/10.1103/5pgp-1wj6> for a movie of the simulation results.
- [25] R. Clayton, O. Bernus, E. Cherry, H. Dierckx, F. Fenton, L. Mirabella, A. Panfilov, F. Sachse, G. Seemann, and H. Zhang, Models of cardiac tissue electrophysiology: Progress, challenges and open questions, *Prog. Biophys. Molec. Biol.* **104**, 22 (2011).
- [26] A. Winfree and S. Strogatz, Organizing centers for three-dimensional chemical waves, *Nature (London)* **311**, 611 (1984).
- [27] J. Keener and J. Tyson, The dynamics of scroll waves in excitable media, *SIAM Rev.* **34**, 1 (1992).
- [28] A. M. Pertsov, M. Wellner, M. Vinson, and J. Jalife, Topological constraint on scroll wave pinning, *Phys. Rev. Lett.* **84**, 2738 (2000).
- [29] D. Gurevich and R. O. Grigoriev, Robust approach for rotor mapping in cardiac tissue, *Chaos* **5**, 093107 (2019).
- [30] M. Duytschaever *et al.*, Atrial topology for a unified understanding of typical and atypical flutter, *Circ. Arrhythm Electrophysiol.* **17**, e013102 (2024).

- [31] S. Verheule, J. Eckstein, D. Linz, B. Maesen, E. Bidar, A. Gharaviri, and U. Schotten, Role of endo-epicardial dissociation of electrical activity and transmural conduction in the development of persistent atrial fibrillation, *Prog. Biophys. Molec. Biol.* **115**, 173 (2014).
- [32] P. C. Bressloff, *Waves in Neural Media: From Single 389 Neurons to Neural Fields* (Springer, New York, 2014).
- [33] C. Luo and Y. Rudy, A dynamic model of the cardiac ventricular action potential; II: Afterdepolarizations, triggered activity and potentiation, *Circ. Res.* **74**, 1097 (1994).
- [34] C. Antzelevitch and A. Burashnikov, Overview of basic mechanisms of cardiac arrhythmia, *Card. Electrophysiol. Clin.* **3**, 23 (2011).
- [35] A. Gobeyn, D. Kabus, E. G. Tolkacheva, and H. Dierckx, ZEUS: Numerical methods to detect quasi-particles describing excitable media (to be published).
- [36] B. Zwiebach, *A First Course in String Theory* (Cambridge University Press, Cambridge, England, 2004).
- [37] D. Kabus, M. Cloet, C. Zemlin, O. Bernus, and H. Dierckx, The ithildin library for efficient numerical solution of anisotropic reaction-diffusion problems in excitable media, *PLoS One* **19**, 1 (2024).
- [38] L. Arno, D. Kabus, and H. Dierckx, Dataset for “Strings, branes and twistons: Topological analysis of phase defects in excitable media such as the heart” (2025), [10.5281/zenodo.16089825](https://zenodo.org/record/16089825)

End Matter

Appendix A: Brief overview of 2D quasiparticle viewpoint—Figure 1(a) depicts a state-space view of excitable elements. The state of each excitable element in the medium can be characterized by $n \geq 2$ local state variables $\mathbf{u} = (u_1, u_2, \dots, u_n)^T$, which together span an n -dimensional state space. In physiology, u_1 is often taken to be the transmembrane voltage. The time evolution in the coupled spatial system is given by a cardiac monodomain model (reaction-diffusion equations) or bidomain model [25]. The system’s excitability makes most points in the medium reside in a state within a torus-shaped attractor $\mathcal{T}$. Within $\mathcal{T}$ lies a prototypical excitation path $\mathcal{L}$, which is the time course of a point that is excited by a plane wave in the medium; see Fig. 1(a). The activation phase ϕ is a coordinate measuring the progress along the torus. States outside $\mathcal{T}$ form less probable zones $\mathcal{Z}$. In excitable systems, excitation has a finite amplitude, and therefore most of the state space belongs to $\mathcal{Z}$. Next, we split $\mathcal{T}$ in an excited region ($\mathcal{E}$, yellow) and an excitable region ($\mathcal{U}$ for unexcited, white). Here, we determine $\mathcal{U}$ and $\mathcal{E}$ depending on whether u_1 exceeds a threshold value u_* or not. The boundary between $\mathcal{E}$ and $\mathcal{U}$ consists of two regions: where u_1 increases, points are exciting. Since these points will lie on a wave front in the spatial domain, we mark this region as $\mathcal{F}$ (in cyan). The points that are changing from $\mathcal{E}$ to $\mathcal{U}$ are marked as $\mathcal{B}$, for wave back (in magenta). Coloring spatial patterns in the same manner leads to Fig. 1(b). In the spatial domain, we use noncalligraphic letters (Z, E, U, F, B) to denote the regions. At conduction blocks, the phase varies rapidly in space and manifests as a PD [12,13] (gray). State space elements far outside the torus attractor were not observed in our datasets but may occur during external stimulation. A wave front always has two end points, which lie either on a PD or on a medium boundary. In both cases, we called these points “heads” [20]. Similarly, we name the end points of a wave back on a medium boundary or PD “tails”. With $\mathcal{C}$ being any

closed contour on which ϕ is defined, the classical topological charge [7,8,20,28],

$$Q = -\frac{1}{2\pi} \int_{\mathcal{C}} d\phi = -\frac{1}{2\pi} \int_{\mathcal{C}} \vec{\nabla} \phi \cdot \vec{dr}, \quad (\text{A1})$$

yields an integer value. If one defines the topological charge $Q = 1/2$ for a head or tail which has the PD to the left when looking in the propagation direction and $Q = -1/2$ otherwise, the sum of head and tail charges matches the classical Q [20]. We denote these points as h^+, t^+, h^-, t^- , respectively. Now, since every wave front or wave back has two end points of different chirality, the total Q -charge over the set of all heads (H) must vanish and similarly over the set of all tails (T):

$$\sum_{h \in H} Q_h = 0, \quad \sum_{t \in T} Q_t = 0, \quad \sum_{j \in H \cup T} Q_j = 0. \quad (\text{A2})$$

The third quasiparticle in 2D theory, the pivot, is found as follows. The points in the physiologically forbidden zone ($\mathcal{Z}$) correspond to regions of ill-defined phase in spatial patterns, the PDs. Typically, the regions of ill-defined phase do not fill parts of the medium, but rather appear in 2D as elongated regions; hence they were also called phase discontinuities [12] or PD lines [13]. In this regime, we can fit a curve to the PD, at which end points the wave front makes a 180° turn. We called these end points the pivots. The local rotation of the wave front around the PD can be quantified using the gradient of local activation time τ : with $\psi = \text{atan2}(\partial_y \tau, \partial_x \tau)$, one can in analogy to Eq. (A1) define the topological charge as [20]

$$P = \frac{1}{2\pi} \int_{\mathcal{C}} d\psi = \frac{1}{2\pi} \int_{\mathcal{C}} \vec{\nabla} \psi \cdot \vec{dr}. \quad (\text{A3})$$

This quantity too evaluates to an integer for any closed contour on which ψ is defined and continuous. A pivot point contributes $P = \pm 1/2$ for (counter)clockwise

TABLE I. Overview of simulation used throughout the paper. Δx and Δt are the space and time steps. Kinetics refer to different cardiac monodomain models: Bueno-Orovio-Cherry-Fenton (BOCF) in epicardial settings (EPI) [22] and Fenton-Karma (FK) in MLR-I settings [19].

Fig.	Δx	Δt	Domain size	Kinetics	D_1	D_2/D_1
1(b)	0.262 mm	0.163 ms	450×450	FK (MLR-I)	$0.1 \text{ mm}^2/\text{ms}$	1
1(c)	0.31 mm	0.1 ms	$375 \times 375 \times 20$	BOCF (EPI)	$0.1171 \text{ mm}^2/\text{ms}$	0.25
1(d)	0.5 mm	0.1 ms	$168 \times 208 \times 231$	BOCF (EPI)	$0.1171 \text{ mm}^2/\text{ms}$	0.25
3(a)	0.31 mm	0.1 ms	$600 \times 600 \times 20$	BOCF (EPI)	$0.1171 \text{ mm}^2/\text{ms}$	0.25
3(b)	0.25 mm	0.009 ms	$1200 \times 1200 \times 20$	BOCF (EPI)	$0.1171 \text{ mm}^2/\text{ms}$	1
3(c)	0.5 mm	0.1 ms	$168 \times 208 \times 231$	BOCF (EPI)	$0.1171 \text{ mm}^2/\text{ms}$	0.25
4	0.5 mm	0.1 ms	$256 \times 256 \times 128$	BOCF (EPI)	$0.1171 \text{ mm}^2/\text{ms}$	1

rotation of the wave, and a topological charge $P = \pm 1/2$ can be assigned to each pivot. Due to the localized nature and preservation over time of heads, tails, and pivots, we suggest calling these quasiparticles or “cardions” [20].

Appendix B: Numerical methods—Parameters and reaction kinetics in numerical simulations: The results presented in this paper are valid for a wide range of excitable systems. For definiteness, we produced the numerical examples in this paper by time-stepping of the reaction-diffusion equations using the Ithildin open source software [37]:

$$\partial_t \mathbf{u} = \Delta \mathbf{P} \mathbf{u} + \mathbf{F}(\mathbf{u}). \quad (\text{B1})$$

Here $\mathbf{u}(\vec{r}, t)$ is discretized using finite differences, and time stepping used the forward Euler method; see Table I for simulation parameters. The matrix of diffusion constants $\mathbf{P} = \text{diag}(1, 0, \dots, 0)$. The reaction-kinetics function $\mathbf{F}(\mathbf{u})$ depends on the model, for which the ones used in this paper are indicated in the corresponding figures and Table I. To include the rotation of myofibers inside the cardiac wall, the Laplacian Δ in Eq. (B1) was replaced by the anisotropic diffusion operator $\nabla \mathbf{D} \nabla$ with $\mathbf{D}$ a 3×3 -matrix with elements $D^{ij} = D_1 \delta^{ij} + (D_1 - D_2) e_f^i e_f^j$, $i, j \in \{1, 2, 3\}$. Here, δ^{ij} represents the Kronecker delta. The values of the diffusivities D_1 and D_2 and the orientation of the fiber direction $\vec{e}_f$ depend on the different examples, indicated in the corresponding figures.

Postprocessing: We used the linear activation-time based phase [20]:

$$\phi(\vec{r}, t) = \begin{cases} 2\pi \frac{\tau(\vec{r})}{\tau_0} & \tau(\vec{r}) < \tau_0 \\ 2\pi & \tau(\vec{r}) \geq \tau_0 \end{cases}, \quad (\text{B2})$$

with $\tau(\vec{r})$ being the last local activation time. Wave fronts and backs were selected as the isochrones which indicate the transition of going from an excited region E, defined as $u_1 > u_*$ to an unexcited region, defined as $u_1 \leq u_*$.

The distinction between front and back was done via a second threshold R_* . Both values of u_* and R_* depend on the reaction kinetics and will be given below for each example. Phase defects were tracked as the points for which the phase coherence [21] is above a threshold, depending on the chosen model. The positions of heads and tails were calculated as the points where fronts or backs touch a phase defect, respectively. The pivots were manually annotated as the points where the curvature of the circumference of the phase defect was extremal. The positions of heads, tails and pivots were drawn manually on the 2D simulation results. An automated annotation will be the topic of a subsequent publication [35].

The Möbius-strip shaped PDS from Fig. 4 was created similarly as one would make it with a sheet of paper: We sampled frames from half a rotation of a linear-core spiral wave in the 2D BOCF model, isotropic medium, and pasted them along a circle in cylindrical coordinates in 3D while rotating the solution over 180° when traversing the circle. To this aim we used toroidal coordinates (r, θ, ζ)

$$x = (R + r \cos \theta) \cos \zeta \quad (\text{B3})$$

$$y = (R + r \sin \theta) \sin \zeta \quad (\text{B4})$$

$$z = r \sin \theta. \quad (\text{B5})$$

If $\mathbf{u}_0(\rho, \phi, t)$ is a 2D linear-core solution in polar coordinates (ρ, ϕ) with period T and the middle of the core (PD line) at $x = 0$, $y = 0$, then we take as initial conditions

$$\mathbf{u}(r, \theta, \zeta) = \mathbf{u}_0\left(cr, \theta + \frac{\zeta}{2}, \frac{T\zeta}{4\pi}\right), \quad (\text{B6})$$

with radial scaling factor $c = 4/3$ and average strip radius $R = 32 \text{ mm}$. This initial condition immediately created a Möbius scroll, which remained stable but precessed during the length of the simulation (about 10 rotations); see Supplemental Movie [24].