Spatial patterns of activity, in particular spiral waves, are observed in a broad class of physical, biological and chemical excitable systems \[1\]. One of the most important contexts in which spiral waves occur is that of electrical activity in the heart, where they can act as local sources of high-frequency excitations. This disrupts the rhythmic pumping action of the heart, leading to irregularities known as arrhythmias \[2\]. Understanding the dynamics of spiral waves may potentially result in improved methods for controlling such arrhythmias \[3, 4, 5, 6, 7, 8\]. Spatial wave dynamics, primarily characterised by the motion of its core (i.e., the trajectory of the spiral wave tip, defined to be a phase singularity) can be either stationary rotation, or, evolving with time as in the case of meandering and drift \[9\]. Drift, which has a significant linear translational component, is a possible underlying mechanism for polymorphic ventricular tachycardia \[4, 9\]. This arrhythmia, which is characterised by an aperiodic electrocardiogram, can be a precursor of fully disordered activity in the heart, where they can act as local sources of high-frequency excitations giving rise to turbulent activity in the heart.

Electro-physiological heterogeneities in cardiac tissue may arise, in general, through spatial variation in the ionic currents of the excitable cells. There can also be gradients in the inter-cellular coupling as a result of the inhomogeneous distribution of the conductances of gap junctions connecting neighboring cells. In this paper, we use a simple model of cardiac tissue to investigate the role of these types of heterogeneities in governing the direction of the spiral wave drift. We report the existence of a regime where the spiral wave core moves towards the region with higher excitability. This is a novel finding, never before observed in a model of excitable media and may arise, in general, through spatial variation in the ionic currents and intercellular couplings. For this purpose, we introduce the parameters \( \alpha \) and \( \gamma \), which represent the spatial variation in ionic currents and conduction properties (respectively) for an inhomogeneous distribution of the conductances of gap junctions connecting neighboring cells. In this paper, we study the effects of heterogeneous distribution of the ionic currents and intercellular couplings. For this purpose, we introduce the parameters \( \alpha \) and \( \gamma \), which represent the spatial variation in ionic currents and conduction properties (respectively) for an inhomogeneous distribution of the conductances of gap junctions connecting neighboring cells.
medium. Parameter $\alpha$ directly scales the value of the ionic current in Eq. 1 while $\gamma$ scales the diffusion coefficient as $D = D_0 + \gamma(x) \ (D_0 = 1$ for the rest of the paper). In this study, we have used the Barkley model \[22\], where the several gating variables are aggregated into a single variable $g$ that controls the slow recovery dynamics of the medium with $F(V, g) = V - g$. The nonlinear dependence of the ionic current on the fast variable $V$ is represented by the cubic function $I_{ion} = [V(1-V)(V-(a+b))/\epsilon]$, where $a$ and $b$ are parameters governing the local kinetics and $\epsilon$ is the relative time scale between the local dynamics of $V$ and $g$. The spatial heterogeneity of local excitability and cellular coupling are assumed to have linear functional form, viz., $\alpha(x) = \alpha_0 + \Delta\alpha \ x$ and $\gamma(x) = \gamma_0 + \Delta\gamma \ x$. The variable $x$ represents the spatial position along the principal direction of the inhomogeneity gradient, the origin being considered to be the initial position of the spiral wave tip. At this point, $\alpha = \alpha_0$, $\gamma = \gamma_0$, and $\Delta\alpha, \Delta\gamma$ measure their rate of change along the gradient. For all the figures in this paper, we have used $\alpha_0 = 1.15$ and $\gamma_0 = 1.3$.

The two dimensional system is discretized on a square spatial grid of size $L \times L \ (L = 200$ for the figures shown here). The values of space step $\Delta x$ and time step $\Delta t$ used are 0.5 and 0.005 respectively. A sample of simulations have been repeated for $\Delta x = 0.25$ to verify numerical accuracy. The model equations are solved using forward Euler scheme with a standard 5-point stencil for the Laplacian. No-flux boundary conditions are implemented at the edges of the simulation domain. The initial condition for all simulations is a stable non-meandering spiral, the spiral tip being at the centre of the simulation domain.

Increasing either the ionic current (via $\alpha$) or intercellular coupling (via $\gamma$) results in increasing the excitability of the medium. Thus, to investigate the role of heterogeneity in spiral drift, we have considered spatial gradients in $\alpha$ or $\gamma$ individually (keeping the other parameter constant). After extensive numerical simulations that scan over the $(a, b)$ parameter space of the Barkley model, we have found that it is indeed possible to observe anomalous drift of the spiral, i.e., drift towards regions with higher excitability (shorter periods). An example of such anomalous drift is shown in Fig. 1(A,C). For comparison, in Fig. 1(B,D) we show the normal drift of the spiral towards regions of lower excitability. This is seen for a set of $(a, b)$ values which is farther from the boundary with the sub-excitable region of the Barkley model \[22\] than the $(a, b)$ parameter set for which anomalous drift is observed in Fig. 1(A,C).

To analyse the genesis of anomalous drift, we first look at how the parameters $\gamma$ and $\alpha$ affect the spiral wave in an homogeneous medium. As $\gamma$ is only a scaling factor for the diffusion coefficient, the period of the spiral wave does not depend on it. Further, scaling arguments suggest that the spiral wavelength increases as a square root of $\gamma$. Thus, for normal drift in the presence of a gradient in $\gamma$, the spiral moves towards the shorter wave-length region, while for anomalous drift, it is directed towards longer wavelengths. Fig. 2 shows the variation of the spiral period and wavelength as a function of the parameter $\alpha$, both of which decrease as $\alpha$ increases \[24\]. From these results we can infer that, for normal drift in the presence of $\alpha$ gradient, the period and wavelength of the spiral increase as the core moves towards lower $\alpha$ regions. In contrast, we see a decrease in the period and wavelength in the case of anomalous drift towards regions having higher values of $\alpha$.

Next, we study the effect of the magnitude of spatial gradient in $\alpha$ or $\gamma$ on the velocity of spiral drift. Fig. 3 shows the longitudinal component of the drift velocity, $V_L$, i.e., along the gradient, as a function of the spatial variation in $\alpha$ or $\gamma$. Note that, positive $V_L$ corresponds to anomalous, while negative $V_L$ corresponds to normal drift of the spiral wave. Fig. 4 shows that, for normal drift, increasing either of the gradients results in a monotonic increase of $V_L$. However, in the case of anomalous drift as a result of $\alpha$ gradient, we see a non-monotonic behavior in $V_L$, which first increases but then decreases and becomes negative (Fig. 4a). Thus, the anomalous drift of the spiral towards higher excitability in $\alpha$ gradient is seen only for small $\Delta\alpha$. For higher $\Delta\alpha$, there is a reversal of direction and the spiral exhibits normal drift. On the other hand, Fig. 4(b) shows that for a gradient in $\gamma$, the anomalous drift is observed for the entire range of $\Delta\gamma$ that is investigated.
of anomalous and normal drift, respectively, in presence of a gradient in $\alpha$. The solid and broken arrows represent the directions of anomalous and normal drift, respectively, in presence of a gradient in $\alpha$.

We have also studied the effect of the local kinetics on anomalous drift by varying the Barkley model parameter $a$ (Fig. 4). Increasing $a$ (keeping $b$ fixed) decreases the activation threshold of the medium, and thus makes the system more excitable. We observe that for both $\alpha$ and $\gamma$ gradients, the variation of $V_L$ as a function of $a$ is non-monotonic. For the cellular coupling ($\gamma$) gradient, the presence of anomalous regime clearly correlates with excitability. The drift is anomalous at lower excitabilities, the drift becomes normal.

Therefore, the heterogeneous cellular coupling $\gamma(x)$ contributes to both the gradient ($\partial\gamma/\partial x$) and second order ($\gamma(x)\nabla^2 V$) terms. The relative contributions of these terms to the longitudinal component of drift velocity is shown in Fig. 4 (b). We observe that the principal effect on $V_L$ is due to the $\partial\gamma/\partial x$ term, while $\gamma(x)\nabla^2 V$ accounts only for about 10% of the observed drift. This allows us to propose the following explanation for anomalous drift in the presence of a gradient in $\gamma$. If we do not consider the $\gamma(x)\nabla^2 V$ term in the Laplacian, the spatial operators in Eq. (1) can be expanded as,

$$V_L = \nabla \gamma(x) D V = (D_0 + \gamma(x))\nabla^2 V + \partial\gamma/\partial x \partial V/\partial x + \partial^2 \gamma/\partial x^2 \partial^2 V/\partial x^2. \quad (3)$$

Fig. 2: The variation of spiral period and wavelength as a function of the parameter $\alpha$. The symbols “1” and “2” correspond to the values of $\alpha$ in the region around the initial and final positions (respectively) of the spiral waves in Fig. 1 with the same sets of Barkley model parameters being used. The solid and broken arrows represent the directions of anomalous and normal drift, respectively, in presence of a gradient in $\alpha$.

Fig. 3: Drift velocity depends on the gradient in parameters $\alpha$ and $\gamma$. (a) Non-monotonic variation (solid curve) of the longitudinal component of spiral wave drift velocity $V_L$ as a function of the gradient in local excitability, $\Delta\alpha$, for a model system with parameters $a = 0.82$, $b = 0.13$. Positive values of $V_L$ indicate anomalous drift. For a different set of parameters ($a = 1.02$, $b = 0.15$), normal drift is seen for the entire range of gradients used (broken curve). (b) Variation of $V_L$ with the gradient in cellular coupling, $\Delta\gamma$. Solid and broken curves represent the anomalous and normal drift seen for the two parameter sets mentioned earlier (respectively), and are observed throughout the range of gradients used.
The occurrence of scroll expansion in 3-D implies the existence of anomalous drift in γ gradient in 2-D. Conversely, observation of anomalous drift might suggest parameter regions where scroll wave expansion is possible.

In this paper, we have explicitly demonstrated the possibility of spiral waves to drift towards region of higher excitability in a simple model of heterogeneous excitatory medium. Most of the detailed ionic models for cardiac tissue have the same form as Eq. (1) and, therefore, our analysis can be easily extended to biologically realistic models, such as LR1 or TNTP [31, 32]. It might be possible to infer the parameter range in realistic models where anomalous drift may occur by using the relation between the cellular coupling gradient induced drift and scroll ring expansion. Note that, the latter phenomenon has recently been seen in the LR1 model [22].

Spiral waves are not only relevant for cardiac tissue, but are also observed in many different excitable media. Thus, it may be possible to relate our observations with results of kinemetic studies and models of cyclic catalysis in replicating entities [32], which predict drift towards region with shorter periods. From a clinical perspective, anomalous drift is important as it clearly promotes arrhythmia and may result in fibrillation by promoting wave-breaks away from the spiral core. Spiral drift in the presence of a cellular coupling gradient may be a key factor giving rise to abnormal wave activity in regions of the heart where conductivity changes abruptly, e.g., at Purkinje-muscle cell junctions or in an infarct border zone [32]. It can also be studied experimentally and numerically in many model systems, such as, heterogeneous mono-layers of neonatal rat cardiomycocytes [34].

To conclude, we have observed that spiral waves in heterogeneous excitable media can drift towards regions having higher excitability. Such anomalous drift occurs either in media having intermediate to low excitability when the heterogeneity is a gradient in ionic current, or, in media with low excitability for a gradient in the cellular coupling. Further, it appears to be related to regimes where expansion of 3-dimensional scroll wave filaments is observed. Anomalous drift of spiral waves may increase the likelihood of the onset of complex spatio-temporal patterns in excitable medium, e.g., turbulent electrical activity in the heart.

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