Capture of fixation by drifting phase singularities; a neurodynamical hypothesis of fixational drift and tremor

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ABSTRACT
During visual fixational, the eye is in constant motion. Recently, high resolution recordings of fixational eye movements have revealed a previously unsuspected amount of substructure. The generative mechanisms of drift and tremor, the movements which occupy most of fixation time, are currently unknown. The trajectory of fixational drift and tremor bear dynamical similarities to the behaviour of the phase singularity about which neural spiral wave formations rotate, motivating the current hypothesis that drift and tremor reflect the capture of fixation by drifting spiral neurodynamics. Spiral wave dynamics are ubiquitous in nature and have been observed in many biological systems including the brain and visual cortex. These rotating waves play an organizational role in dynamical systems at many scales, and have been observed in both normal and pathological biological conditions. In this purely theoretical review and hypothesis paper, we motivate our hypothesis in terms of the existing literature, and make predictions could falsify it.

Keywords: active vision, fixational eye movement, drift, tremor, neurodynamics, travelling waves, spiral wave, phase singularity

1 INTRODUCTION
During fixation the eye is not still. Three main classes of fixational eye movement (henceforth FEM) have been identified (Martinez-Conde et al., 2004). Microsaccades are very fast movements which occur relatively infrequently. Drift is a slow, meandering component which occupies most of fixation time. Tremor is a fast, low amplitude aperiodic oscillation imposed on drift. Microsaccades are in many ways much like saccades on a tiny scale (Ko et al., 2010; Otero-Millan et al., 2013; Kagan and Hafed, 2013; Martinez-Conde et al., 2013; Poletti et al., 2013), though they may also be linked to the drift component (Engbert and Mergenthaler, 2006; Engbert et al., 2011). The neural basis of drift and tremor is unknown (Martinez-Conde et al., 2004), but these movements may play important functional roles in vision (Rucci et al., 2007; Kuang et al., 2012; Ahissar and Arieli, 2012). Recently, very high resolution eye movement data based on tracking tiny movements of ocular vein structure in three dimensions has revealed more structure to FEM than had previously been suspected (Zhang and Li, 2012; Li and Zhang, 2012). These studies reported microsaccades which were not straight and ballistic (as previously thought), but bent and jerky. Relatively little detailed information was given, but Zhang and Li (2012) reported that the drift-tremor combination took a complex, curling trajectory.
These high resolution data may enable new insight into the underlying generative mechanisms of fixational eye movements. The findings of Zhang and Li (2012); Li and Zhang (2012) inspire our renewed interest in earlier related work from our group (Wilkinson and Metta, 2011; Wilkinson et al., 2011), and motivate the current hypothesis that fixational drift and tremor reflect the capture of fixation by drifting spiral wave neurodynamics. If fixation between microsaccades tracks the central phase singularity of a drifting spiral wave (Winfree, 1991), then complex, curling fixational drift-tremor trajectories would be a natural outcome.

We have aimed to keep the current discussion concise and on topic, with only a few brief digressions to potentially interesting connections to the wider literature. Sections 2.1 and 2.2 examine the biological and ecological plausibility of the singularity hypothesis based on the existing literature. Our purpose is not an exhaustive review, but a targeted presentation of a few lines of evidence which render our hypothesis interesting, plausible and worth testing. Section 2.3 points to a few interesting related lines of inquiry being followed up in our planned and ongoing work. Section 3 details the predictions implied by the singularity hypothesis of fixational drift and tremor. Section 4 concludes the paper.

2 BIOLOGICAL AND ECOLOGICAL PLAUSIBILITY OF THE SINGULARITY HYPOTHESIS

2.1 BIOLOGICAL PLAUSIBILITY

2.1.1 Spiral waves in nature The multiscale ubiquity of spiral waves in nature and biology (Toomre, 1969; Lechleiter et al., 1991; Winfree, 2001), and their interesting dynamical properties (Boerlijst and Hogeweg, 1991; Biktashev and Holden, 1993, 1995; Langham and Barkley, 2013), have motivated many physical, chemical and mathematical studies. Important contributions to theoretical understanding of coupled oscillating systems were provided by Kuramoto (Kuramoto and Tsuzuki, 1976), and many physical and biological systems have been modelled using the theory of coupled oscillators and the complex spatiotemporal travelling wave formations which manifest in coupled oscillator networks (Kuramoto, 2003; Acebrón et al., 2005). Arthur Winfree pioneered computational and empirical investigations of toroidal dynamics in chemical and biological systems (Winfree, 1967, 1972). Many biological dynamics exhibit toroidal form (Winfree, 2001). The modern understanding of pathological heart fibrillation (and de-fibrillation intervention) is perhaps the most prominent medical application of this work e.g. (Gray et al., 1998; Gray and Chattipakorn, 2005; Breakspear et al., 2010), though cellular calcium transmission is another important example (Lechleiter et al., 1991). Spirals are reentrant waves which circle around a central rotor known as a phase singularity (Winfree, 1991); a point of maximally uncertain phase, surrounded by points of all phases. The central rotor of a whirlpool or tornado provides a physical example in three dimensions.

2.1.2 Spiral waves in the brain Spiral and other travelling waves have been observed via voltage sensitive dye imaging (VSDI) of mammalian visual cortex under certain conditions (Huang et al., 2004, 2010), and widely in various species under visual stimulation (Wu et al., 2008; Sato et al., 2012). VSDI is an invasive optical imaging method which enables measurement of subthreshold changes in membrane potential with high spatiotemporal resolution (Grinvald and Hildesheim, 2004). Spiral dynamics are commonplace in the dynamics of simulated excitable media including networks of model neurons (Milton et al., 1993; Winfree, 2001; Yu et al., 2010; Chun-Ni et al., 2010; Ma et al., 2012). Movies of real cortical spiral waves in the VSDI signal (from Huang et al. (2010)) can be found here. It has been suggested that spiral waves (also termed vortices) play an organising role in neural field interactions (Freeman, 2009; Huang et al., 2010). Short-lived spiral waves are frequently observed in the healthy case (Huang et al., 2010), but the growth of spiral wave formations of large duration and extent has been linked to pathological conditions including heart fibrillation (Gray et al., 1998) and epileptic
seizure (Stacey, 2012). This is suggestive that spiral waves are a part of normal function, whether constitutive or epiphenomenal, but that their (potentially useful) tendency to enslave surrounding dynamics (e.g. Savill et al. (1997); Yang and Yang (2007); Huang et al. (2010)) has to be carefully controlled.

2.1.3 Dynamical behaviour of spiral waves The dynamical behaviour of spiral waves can be complex and is the subject of extensive research. A useful introduction with video visualisations is given at Björn Sandstede’s website hosted by the Dept. of Applied Mathematics at Brown University, USA, linked here. At the risk of oversimplifying, the behaviour of spiral waves exhibits three basic components. Firstly, the rotational orbit of the whole spiral wave will exhibit a characteristic frequency and phase, and is reflected in a small, “on the spot” circular rotation of the phase singularity at the spiral tip. The current hypothesis proposes that this component may explain new high resolution observations of curling trajectories of drift and tremor (Zhang and Li, 2012; Li and Zhang, 2012).

This trajectory may be perturbed in various ways to take on a locally more complex, globally drifting form. This is known as spiral drift, and occurs in response to various forms of symmetry breaking perturbations/gradients in the external milieu (Biktashev and Holden, 1995; Wulff, 1996; Sandstede et al., 1999; Biktashev, 2007). Figures 1-11 in the Scholarpedia article Biktashev (2007) (linked here), display images and animated movies of the trajectory of spiral singularities under various forms of symmetry breaking. Note the basic curling trajectory, whose period is equal to that of the wave’s orbit, typically around the alpha range in cortex (Huang et al., 2010). Perturbations can push this orbit this way or that. This spiral drift in response to perturbations is the neural correlate we hypothesise for the well known slow component of fixational drift.

In addition to the above relatively slow components, fast, aperiodic oscillatory modulations of the basic curling trajectory can result from instabilities at the phase singularity (Winfree, 1991). Gray et al. (1998); Bray et al. (2001) tracked the spatiotemporal trajectory of phase singularities in cardiac fibrillation data. Figure 1, from Bray et al. (2001) depicts the evolution of a real cardiac phase singularity (white tube inside black mesh) in detail over one cycle of the carrying spiral wave. Figure 2, also from Bray et al. (2001) graphs longer trajectories of the singularities of four interacting spirals. Note the aperiodic, gamma range oscillation superimposed on the basic curling trajectory, much faster than the period of the carrier wave. Gray et al. (1998) reported similar spiral meander in the gamma range during cardiac fibrillation. Though here in cardiac tissue rather than sensory cortex, this instability at the singularity is a universal feature of spiral waves (Winfree, 1991). The current proposal suggests this instability as the source of the well known high frequency component of fixational tremor.

2.1.4 Dynamical characteristics of fixational eye movements Microsaccades are the most intensively researched component of FEM, but their control is not our current focus. These fast relocations of the fixation point appear to play a similar role and activate similar brain regions as saccades more generally (Ko et al., 2010; Hafed and Krauzlis, 2012; Otero-Millan et al., 2013; Kagan and Hafed, 2013; Martinez-Conde et al., 2013; Poletti et al., 2013), but also show relations to drift (Engbert and Mergenthaler, 2006). Microsaccades are relatively infrequent, occurring around three times per second at most and usually less frequently, in an irregular but individually characteristic fashion (Engbert and Mergenthaler, 2006). As those authors note, explaining the intra and inter individual variability of microsaccade occurrence is a challenge for any model of FEM. Most of fixation time (> 90%) is occupied by a slow (< 3mm/s, usually in the lower end of this range), quasi-persistent drift, as depicted in Figure 3. Upon this is superimposed a fast (around 90Hz), low amplitude (approx. one photoreceptor), aperiodic oscillation termed tremor. The generative mechanisms of drift and tremor are unknown (Martinez-Conde et al., 2004), and are the focus of this paper.
Recently, Zhang and Li (2012) reported technical innovations which enable non-invasive imaging of FEM in three rotational degrees of freedom, by very high resolution binocular video tracking of ocular vein structure. Figure 4 depicts a classical schematic conception of FEM trajectories (from Pritchard, 1961) compared to a real trajectory, taken from Zhang and Li (2012). Those authors reported a previously unsuspected level of structure at high resolution. Microsaccades were neither straight nor ballistic, a fascinating finding, but one which does not concern us greatly in the current paper. Crucially to the current hypothesis, drift and tremor traced a complex, curling trajectory. A drift-tremor trajectory which is exploratory on the macro scale, persistent on the meso scale, and complex and self-crossing on a small scale is a fairly distinctive dynamical signature, and one that is shared by drifting spiral singularities.

2.1.5 Are FEM tremor and drift expressions of spiral wave meander and drift?

The velocity profile of fixational drift (Ezenman et al., 1985; Zhang and Li, 2012) and that of spiral drift in visual cortex in vivo (Huang et al., 2010) are well matched in the range up to around 3mm/s, usually in the lower end of this range. Like FEM drift, the velocity of spiral drift in neocortex is variable, and was found to be higher in induced sleep-like states than under local chemical disinhibition (see Figure 5), consistent with recent observations that time-on-task increases the speed of FEM drift, whilst reducing the peak velocity of microsaccades (Di Stasi et al., 2013). Figures 3 and 5 display low resolution fixational and spiral drift trajectories respectively, for visual comparison. Engbert et al., (2011) found that drift trajectories were well described as a self-avoiding random walk at a certain level of resolution. Spiral drift can take on the characteristics of Brownian motion under certain conditions (Biktashev and Holden, 1998; Sendina-Nadal et al., 2000; Yuan et al., 2011).

Tremor movements occur on a much faster scale than drift, roughly corresponding to the mid-high gamma range (Ditchburn and Ginsborg, 1953; Ezenman et al., 1985; Zhang and Li, 2012), which maps quite well to the range of spiral meander, at least in cardiac tissue Gray et al., (1998); Bray et al., (2001). Further, both share an aperiodic nature. Thus FEM drift and tremor may be manifestations of spiral wave drift and meander. The low amplitude, alpha range circular orbit of the spiral carrying wave may help to explain the low amplitude curling component of drift-tremor eye movement reported by Zhang and Li (2012). A low amplitude (approx. 1 photoreceptor), relatively slow (around 5Hz) quasi-periodic oscillation has been reported in the turtle (Greschner et al., 2002), possibly corresponding to this component (note though that FEM can be quite different between species).

2.1.6 Spiral wave death: a potential trigger for microsaccades?

The current contribution focuses on drift and tremor. We do not attempt to address the neural control of microsaccades here. Nonetheless, microsaccades are naturally relevant to the discussion as a whole. Microsaccades occur irregularly, and rates exhibit individual differences which in turn reflect individual differences in drift dynamics (Engbert and Mergenthaler, 2006). Microsaccade onset is preceded by a dropoff in drift velocity Engbert and Mergenthaler (2006). Under the present hypothesis, the most likely trigger for a microsaccade would be the break up of the spiral formation currently capturing fixation, thus “releasing” fixation. The drop-off in drift velocity preceding microsaccades might then reflect the extinction of the carrying spiral wave. Spiral waves are inherently unstable (Winfree, 2001; Sandstede et al., 2000) and have limited lifespan in neural networks (Chun-Ni et al., 2010). Huang et al. (2010) found that most cortical spiral waves were shortlived (1-3) cycles, while a smaller minority persisted for up to 26 cycles. Given cycles in a range around 10Hz, the lifetime range of longer lived spirals (around 0.3-5
2.2 ECOLOGICAL PLAUSIBILITY

2.2.1 Spiral waves during ecological vision?

In order for capture of fixation by spiral wave singularities to be a plausible hypothesis, spiral wave formation must occur under the normal conditions of visual fixation. Propagating waves (also known as travelling waves) are frequently observed both endogenously under disinhibition (Huang et al., 2004, 2010) and during sensory events, see for example Precht et al. (1997); Gao et al. (2012), and for review Wu et al. (2008); Sato et al. (2012). The formation of travelling waves is highly dependent on predominance of local excitation (Winfree, 2001; Sato et al., 2012). Excitatory lateral functional connectivity in visual cortex is inversely proportional to levels of local contrast energy (Nauhaus et al., 2008). In widely used divisive normalisation models (Carandini et al., 1997; Vinje and Gallant, 2000; Carandini and Heeger, 2011), the level of the inhibitory divisor depends on a sum of activity over some relatively large region. Thus in natural scenes with widespread stimulation, the formation of spiral waves may require special conditions under which the inhibition/normalisation field becomes weak. Freeman (2007, 2009) provide theoretical and empirical descriptions of potentially related epoch dynamics.

One possible scenario for this is given by adaptation through predictive coding (Rao and Ballard, 1999; Hesselmann et al., 2010; Bastos et al., 2012; Moran et al., 2013; Lieder et al., 2013). As sensory activity is “explained away” by predictive endogenous activity, the normalisation field is in turn reduced, because it reflects the sum of unexplained activity in some region. The remaining unexplained activity patterns are then more able to propagate and interact laterally as travelling waves. In general, unexplained sensory flow carries the most information with respect to the generative model structuring prediction, and is hence a sensible target for attentional actions such as fixation (Friston et al., 2012a). Other possibilities likely exist.

2.2.2 How would spiral formation mediate amplified sensory salience?

A further plausibility requirement for the singularity hypothesis is the existence of mechanistic means by which spiral formation can increase the salience of its locality on the sensory surface. Spiral wave activity is observed in the VSDI signal, at sub-threshold amplitudes (Grinvald and Hildesheim, 2004). Thus these waves do not in themselves often cause firing, but they can keep the cell in a depolarised “ready” state for input, or indeed polarise the cell to effectively ignore input. This implements a form of gain control, widely agreed to be a fundamental aspect of neural processing generally (Hillyard et al., 1998; Salinas and Thier, 2000; Salinas and Sejnowski, 2001; Rothman et al., 2009; Olsen et al., 2012) and attentional selection in particular (Aston-Jones and Cohen, 2005; Saalmann and Kastner, 2009; Sara and Bouret, 2012). Adaptive tuning of the spike response properties of local cells via polarisation/d depolarisation of the cell membrane is perhaps the most frequently suggested functional role for the neural field dynamics observed in the VSDI signal. See Huang et al. (2010) and Wu et al. (2008) for review. Huang et al. (2010) found that spirals drifted much faster in vivo than in vitro, and that the locus of depolarisation at the spiral centre was much larger in vivo than in vitro, suggestive of active modulation and functional relevance in the intact brain. Many studies, for example Schrader et al. (1995); Wulff (1996); Sandstede et al. (1999); Biktašhev (2007), describe methods by which spiral drift may be altered, offering options for top-down, lateral and bottom-up attentional modulation.

On this view, fast, aperiodic spiral meander depolarises a point locus of local cells in the gamma band in a phase insensitive manner. The region outside the spiral centre is polarised and depolarised periodically by the spin of the spiral arms, on a slower (alpha) scale dependent on the period of the spiral orbit and the number of spiral arms. Examining the relationship between local field potential and spike rates in the temporal cortex, Zanos et al. (2012) found two populations of cells with just these response characteristics. One population responded at high (gamma range) frequencies in a phase invariant manner,
the other at lower (alpha range) frequencies in a phase dependent manner. Whether spiral meander might contribute directly to the form of gamma band bursting, or plays a purely facilitating depolarisation role, is beyond the scope of this paper.

An interesting analogy is of the whole sensory surface (e.g. primary visual cortex) as an adaptive, semi-porous excitable membrane. Drifting spiral singularities on the global membrane surface open localised channels through which sensory signals may selectively pass, by depolarisation of local cell membrane potentials. Thus the pattern of spiral waves on the sensory surface, and their individual and collective dynamics implement a potentially complex, dynamic spatiotemporal filter. This analogy is interesting in highlighting the possibility of shared computational principles between different scales and domains of adaptive filtering and membrane dynamics in the nervous system (Lechleiter et al., 1991; Atri et al., 1993; Chay et al., 1995).

2.2.3 Are spiral waves useful indicators of visual salience?

Besides the mechanistic requirements just mentioned, our hypothesis also requires that spiral wave formation be a functionally effective salience indicator, such that fixation follows a sensible trajectory in terms of gathering information about the world. This aspect is currently the least researched requirement, and the most speculative aspect of the current hypothesis. As a result, it forms the focus of our ongoing work on the current topic, from the perspective of active perception in embodied robotics (Morse et al., 2011).

Laser phase imprinting has been employed to prepare topological states in perfect oscillatory media with great precision (Williams and Holland, 1999; Leanhardt et al., 2002). By analogy, in exploratory work we allowed the visual input to “prepare topological states” in an harmonic oscillatory medium representing an abstract “sensory surface”, which might map to primary visual cortex, lateral geniculate nucleus, or retina (Wilkinson and Metta, 2011; Wilkinson et al., 2011). We simplified to an imprinting event and a relaxation epoch in a two dimensional, harmonic oscillatory medium with local coupling. During the imprinting stage, the spatial phase landscape is set to be that of the centre-surround filtered grayscale input image. During the relaxation phase, the stimulus drive and inhibitory surround is removed and the dynamical system evolves towards some attractor region according to local lateral interactions. Though pure plane wave solutions are possible given simple stimuli such as square wave gratings (Wilkinson and Metta, 2011), the relaxation dynamics of the phase landscapes imprinted by natural images were in all cases structured by spiral singularities, which we used as attractors for a “virtual” visual fixation point. Lateral interactions exhibit a sensitivity for local shape, enacted in terms of the wave forms which result from the imprinting of particular spatial patterns of contrast. See also Haken (2004); Tyukin et al. (2009) for related approaches to pattern perception.

2.2.4 Summary sketch of a contextual setting

The current model envisages the inter-saccadic epoch along the following lines (intended as a rough sketch of a plausible contextual setting, not a prescriptive prediction). A saccade “lands”, and the the decorrelated visual image is imprinted to the oscillatory/excitable sensory surface as a spatial pattern of phase. A relaxation period then occurs, during which fixation is temporarily captured by a spiral singularity, which drifts according to symmetry breaking gradients in the surrounding neural medium. At some point, the spiral wave’s self-production fails and the wave is extinguished and dissipates. This might be due to endogenous failure or outside influence or both. A microsaccade either triggers or is triggered by spiral death (or both), and terminates in capture by a new singularity in the vicinity. The process then repeats until the next saccade relocates the eye, and then begins again. Many different instantiations of this broad sketch are possible. The “cinematic” frame-like chaos suggested by Freeman (2007) provides one possible example.
2.2.5 Chaotic itinerancy  The travelling wave solutions which evolve during relaxation are a function of both the intrinsic dynamics of the system and the initial conditions set by the visual input, and may in many cases be expected to follow a chaotic course (Sandstede et al., 1999). During the inter-saccadic epoch, the fixation point “observes” this system, by sequentially adopting (i.e. enactively sampling) the dynamics of a subset of localities in the system. On this view, the trajectory of fixational eye movement would be characterised by (embodied) chaotic itinerancy (Tsuda, 1991; Kaneko and Tsuda, 2003; Ikegami, 2007), the sequential exploration of a landscape riddled with temporary, competing attractors and attractor ruins (here manifesting as spiral singularities and dead spirals, respectively). This may provide links between FEM and some existing neurodynamical approaches to action-perception (Tsuda et al., 2001; Haken, 2004; Rabinovich et al., 2008; Breakspear et al., 2010; Friston et al., 2012b). If FEM and the itinerant neurodynamics thought to underly perception in these approaches take similar form, then FEM might be able to play a rather sophisticated perceptual role similar to that of neural coding mechanisms (e.g. Rabinovich et al. (2008); Tyukin et al. (2009)), but at the embodied scale wherein the perturbation structure (e.g. light waves, sound waves) of the world is the data set (Ikegami, 2007).

2.3 SPECULATIONS AND ONGOING DEVELOPMENT

The findings of Zhang and Li (2012) motivate our renewed interest in this approach to image processing and visual attention. The potential functional roles of FEM in visual perception are currently a major focus of research. For example, it has recently been shown that FEM decorrelate the visual stimulus stream in a manner optimised with respect to the response properties of retinal ganglion cells (Kuang et al., 2012). Existing work on the more complex dynamics of spiral waves suggests some interesting potential functional benefits of spiral wave FEM and neurodynamics. This section introduces a far from exhaustive taste of the dynamical variety of spiral wave behaviours and how these dynamics might participate in visual perception. If fixational drift and tremor do indeed turn out to be manifestations of the capture of fixation by drifting phase singularities, then these behaviours may turn out to have relevance for biological vision.

2.3.1 Sparsity and travelling wave visual processing  Breakspear et al. (2010) found that travelling wave solutions concentrate the phase frustration of their initial conditions into a few dense regions.

“We believe that local traveling wave structures, which confine the expression of phase frustration to small, isolated locations, represent a globally optimal minimum to this function although we do not provide a proof for this assertion. Were this to be the case, the dynamics (12) could be recast as a gradient descent on the free energy of the system, namely the divergence between the expected pair-wise phase alignment expressed a priori by the coupling function on the r.h.s. of (11) and the dynamical solutions observed a posteriori.”

Breakspear et al. (2010), p.p. 10

The phase frustration/uncertainty at the central singularity of a spiral wave is maximal, as it is surrounded by points of all phases. In the case where the contrast landscape of a visual scene decides the initial conditions (as in Wilkinson et al. (2011)), it may turn out that the travelling wave solutions which emerge during the relaxation phase represent an efficient mode of compression of phase frustration in the contrast image. This may provide a functional justification for travelling wave solutions to visual initial conditions in terms of sparse/efficient coding, a widely used heuristic which implies many features of biological visual perception (Olshausen et al., 1996; Vinje and Gallant, 2000; Hunt et al., 2013; Zhu and Rozell, 2013), and perhaps in terms of free-energy minimisation (Friston, 2010).

2.3.2 Multiscale spatiotemporal filtering by complex spiral wave dynamics?  It is worth noting that the local dynamics of a spiral wave can have interesting global effects. Under certain conditions (destabilization in a Hopf bifurcation (Fiedler et al., 1996)), meander can take on a form wherein the spiral arms
emanating from the singularity at the central tip of the wave are compressed and expanded in such a way (describable by the Doppler Effect) that a superspiral is formed on a larger scale (Perez-Mufiuzuri and Vasiev, 1991; Sandstede et al., 2001; Brusch et al., 2003). See Bjorn Sandstede’s website linked here for visual depictions. On the current view, wherein spiral waves enact spatiotemporal filtering, this behaviour may offer the intriguing possibility for the local trajectories of spiral singularities to mediate scale free adaptive spatiotemporal filtering via the generation of populations of superspirals.

3 PREDICTIONS AND TESTING

Whilst speculative, the singularity hypothesis offers a unified and parsimonious account of fixational drift and tremor, and is consistent with a range of circumstantial evidence from various disciplines. Most persuasive at this early stage, and most easily testable in more detail, are the multiscale dynamical similarities between FEM trajectories and spiral wave dynamics. The singularity hypothesis is interesting in the sense that if true, there may be extensive implications regarding the physiology and function of FEM, and in the sense of providing a bridge between eye movement research and the wider literature on chaotic neurodynamics and the physics of spatiotemporal chaos in oscillatory and excitable media. There may also be more general implications for perceptuomotor coupling and selective attention. It is testable in that it generates strong, detailed and general predictions which could falsify it. These are listed below in order of generality. Prediction 2 is probably the easiest to test. If tests of prediction 2 produce interesting results, then VSDI imaging studies may be worth undertaking.

3.0.3 Prediction 1: Fixation is captured by spiral waves singularities

Whilst their case-to-case details are variable, drift and tremor are universal features of fixation. This strongly suggests that, if the current hypothesis is correct, fixation between microsaccades is always captured by a local phase singularity. This ubiquity might also be suggestive that the “landing” of a microsaccade causes a spiral wave at fixation point. Either way, this provides a very strong general prediction which can in principle be tested with VSDI imaging, though this implies non-human animal studies. Localisation is a more complex question. We concentrate on visual cortex to a certain extent here, partly due to the available evidence from (Huang et al., 2010) and partly due its central role in vision. Primary visual cortex probably presents the best combination of likelihood and accessibility. Visual thalamus and eye movement generators in superior colliculus (Hafed et al., 2009) are also interesting targets, but are less accessible.

3.0.4 Prediction 2: Closer study of fixational drift and tremor will reveal close dynamical relations to spiral dynamics

To date, the results of (Zhang and Li, 2012) have not made a great impact on the wider FEM literature in terms of citations. These findings warrant further investigation. The current hypothesis predicts that further generation and dynamical analysis of high resolution tremor and drift FEM data will reveal a dynamical profile which closely matches that of phase singularity meander and drift in cortical (or perhaps subcortical) spiral waves. At the general level of qualitative dynamics over the whole inter-saccadic period, the singularity model predicts that FEM trajectories will exhibit dynamical signatures of chaotic itinerancy (Tsuda et al., 2001). More specifically, drift and tremor FEM will be better characterised by (at least) three components:

a) The fundamental component of the drift-tremor trajectory will consist of a low amplitude (approx. 1 photoreceptor) quasiperiodic rotational oscillation around the alpha range, corresponding to the quasiperiodic rotational orbit of the phase singularity at the spiral tip.

b) Slow FEM drift will manifest as perturbations of this quasi-periodic carrier wave under symmetry breaking gradients in the external milieu (Biktashev and Holden, 1995; Biktashev, 2007).
c) The fast tremor component will manifest as an aperiodic modulation of the carrier wave caused by the intrinsic instability of the phase singularity (Winfree, 1991).

Figures 6 and 7 depict some phase singularity trajectories in computational simulations, to give a qualitative visual idea of the nature of the drift-tremor trajectory predicted at very high resolution.

3.0.5 Prediction 3: Individual differences in microsaccade rate and drift fractal dimension will reflect individual differences in spiral wave properties

Engbert and Mergenthaler (2006) found that individual differences in microsaccade rates reflected the “exploratory-ness”, quantified as fractal dimension, of individual drift patterns. Under the current hypothesis, these should be reflected in characteristic individual spiral dynamics. Many potential causes of individual differences may exist. For example, spiral drift is sensitive to curvature of the supporting surface (Dierckx et al., 2013). Schwarzkopf et al. (2012) showed that individual differences in gamma band oscillations reflected the physical size of visual cortex. The existence of a relationship between individual gamma characteristics and individual microsaccade rates might be worth examining, as it could provide a testing methodology applicable to humans.

4 CONCLUSION

The neural mechanisms of fixational drift and tremor are currently unknown. We have proposed the hypothesis that these components reflect the drift and meander of spiral wave neurodynamics, on the basis of similarities in their dynamical profiles. Though speculative, this model may offer a parsimonious account of the unexplained complexity observed in new high resolution recordings of drift-tremor trajectories. We have laid out a brief argument motivating our hypothesis in terms of the existing literature, and made testable predictions which could falsify it. Should testing confirm these predictions, there may be more general implications regarding perceptuomotor coupling and the neurodynamics of selective attention.

DISCLOSURE/CONFLICT-OF-INTEREST STATEMENT

The authors declare that no conflict of interest exists.

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SUPPLEMENTAL DATA

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**Figure 1.** The evolution of a spiral wave over one rotational orbit. The black mesh encloses a thresholded area of reduced variance (i.e. low amplitude) at the spiral centre, as observed in cortex by Huang et al. (2004, 2010). The white tube within the black mesh tracks the evolution of the phase singularity at the spiral core. Note the fast (gamma range) oscillation of the singularity, which we hypothesise underlies the gamma range component of fixational tremor. Reproduced from Figure 8b in Bray et al. (2001), copyright John Wiley and Sons Publishing.

**Figure 2.** The evolution of four interacting spiral singularities in space (horizontal axes) over time (vertical axis). Note the fast (gamma range) oscillation of the singularities, which we hypothesise underlies the gamma range component of fixational tremor. Graphs A-C are real trajectories from cardiac data. Graph D is from a computational model. Reproduced from Figure 4 in Bray et al. (2001), copyright John Wiley and Sons Publishing.
Figure 3. Fixational eye movements and microsaccades, from Figure 1 in Engbert et al. (2011). Data were recorded from fixational eye movements during a fixation of 2 s. Slow movements (blue) are highly erratic, whereas microsaccades (red) are ballistic, small-amplitude epochs with a more linear trajectory (compared with the slow background motions). The sample trajectory was recorded with a sampling frequency of 500 Hz (for details see ref. 29 in Engbert et al. (2011)). Image copyright PNAS 2011.

Figure 4. Comparision of a schematic portraying the classical conception of FEM with new high resolution FEM trajectories. From Figure 1 in Zhang and Li (2012).
Figure 5. Behaviour of spiral waves in mammalian visual cortex under various conditions. Drifting of Spiral Phase Singularities. (A) Trajectory of spiral phase singularity during a 12-cycle spiral waves in cortical slices. (B) Trajectory of spiral phase singularity during an 11-cycle spiral waves in vivo under Cch/bic application. Hexagon shows the field of view and each color represents one cycle of spiral wave. (C) Trajectory of spiral phase singularities during 2 spiral waves (red and cyan, each with 1.5 turn) during sleep-like states. (D) Comparison of drifting speed of spiral phase singularity for slices and in vivo. Five examples from in vivo under Cch/bic, in vivo during sleep-like states and slices, respectively, are shown (mean + SD). Columns with stars on top are from the examples in (A)(C). The standard deviation is large because the drifting of spiral phase singularity is not consistent and there are large variations from time to time. The difference between in vivo and slices is statistically significant (Welch’s test, p < 0.001, 25 t tests). The difference between in vivo (Cch/bic) and in vivo (sleep-like) is also significant. Reprinted from Figure 7 in Huang et al. (2010), copyright Elsevier 2010.

Figure 6. Example trajectories of drifting spiral phase singularities in a computational simulation, from Figure 2 in Schlesner et al. (2008). Copyright IOP Publishing 2008.
Figure 7. Further example trajectory of a drifting spiral tip in a computational simulation. From the original; “(a) Spiral wave in the medium 80x80 s.u. large. Darkness of shading shows sum of the values of activator variable u1 and inhibitor variable u2. (b) Same, in the medium 20x20 s.u. The black line is a piece of trajectory of the tip. (c) Piece of the tip trajectory during 40 t.u.; arrows show begin and end of the piece, size of the square is 10x10 s.u., cut from the medium 80x80 s.u”. Reprinted from Figure 1 in Biktashev and Holden (1998), copyright Elsevier 1998.