

Geometric Phase Shift in a Neural Oscillator*

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Abstract

This paper studies the effect of slow cyclic variation of parameters on the phase of the oscillating Morris-Lecar model. In chemical oscillators it is known that a phase shift, called the geometric phase shift, is observed upon return to an initial point in parameter space. We find geometric phase shifts for a two-parameter variation in the Morris-Lecar model. As with the chemical oscillator, the magnitude of the shift is proportional to the area enclosed by the path traced through the parameter space. It is argued that the geometric phase shift may subserve many biological functions. We conclude that the geometric phase shift may be functionally relevant for neural computation.

1 Background

Oscillations are found throughout the nervous system and are believed to play an important role in brain processing (Llinás, 1988). Recent experimental findings indicate that phase information is significant in neural computation involving oscillatory activity. For example, O'Keefe and Recce (1993) found rat hippocampal place cells firing at specific phases of the oscillatory theta rhythm to signal the relative locations of environmental landmarks. Cells firing at an early phase signal the presence of landmarks ahead of the animal, whereas those firing at a late phase signal for landmarks located behind the animal. The utility of phase information is also apparent in other brain areas. In the gamma band, phase information may code for signal strength (Hopfield, 1995) or serve as a binding code (Singer, 1995).

Finding evidence of phase coding as an important factor in oscillatory neural processes suggests the potential significance in neurobiology of the *geometric phase shift*, a well-known phenomenon in Physics (Berry, 1988). When the parameters of an oscillating dynamical system are adiabatically (slowly) varied to trace a closed path in parameter space, a phase shift is observed upon

*This is a DRAFT VERSION of a paper we intend to expand. We welcome any comments or suggestions.
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return to their initial values (Kepler and Kagan, 1991). This phase shift differs from the dynamic phase shift caused by the system’s changing frequency and has a purely geometric origin. It is therefore called the geometric phase shift (also known as *Berry’s phase* in quantum mechanics or *Hannay’s angle* in classical mechanics). The shift is proportional to the integral over the surface in parameter space enclosed by the path traced and depends on the curvature of this surface.

The geometric phase shift is best illustrated by the following quote (Berry, 1988, p. 26):

Take a pencil, lay it on the north pole of a globe and point it in the direction of any of the meridians: the lines of longitude that radiate from the pole. Move the pencil down along the line to the equator and, keeping it perpendicular to the equator, slide it to another line of longitude. Move the pencil back to the north pole along the new meridian, and you will find that although the pencil has returned to its starting point and at no time was rotated, it no longer points along the original line of longitude.

Kagan, Kepler and Epstein (1991) observed geometric phase shifts in a chemical oscillator and proposed that the conditions for the occurrence of the shifts, i.e., the presence of nonlinearities, are sufficiently general to be observable in biological systems as well. To validate their proposal, we investigated the presence of a geometric phase shift in the Morris and Lecar (1981) model. If a geometric phase shift can be demonstrated in this realistic neuron model, it is likely that the principle will generalize to real neurons.

This paper is organized as follows. Section 2 describes the model and how it is used to test for the geometric phase shift. The results of numerical simulations of the model, presented in Section 3, show that the geometric phase shift exists in the Morris-Lecar model. Finally, Section 4 discusses how our findings may be of relevance for neural processing. It is concluded that geometric phase shifts may be relevant for neural computation.

2 Neural Oscillator

In the Morris and Lecar (1981) model the parameter space is spanned by the following set of parameters: $\mathcal{P} = \{v_1, v_2, v_3, v_4, g_{Ca}, g_K, g_L, v_K, v_L, \phi, i\}$. Each of these parameters is associated with biophysical quantities of real neurons. The model may be described in dimensionless form as (cf. Rinzel and Ermentrout, 1989):

$$\frac{dv}{dt} = -g_{Ca} (v - 1) m_\infty(v) - g_K w (v - v_K) - g_L (v - v_L) + i \quad (1)$$

$$\frac{dw}{dt} = \phi (w_\infty(v) - w) \cosh\left(\frac{v - v_3}{v_4}\right) \quad (2)$$

and

$$m_\infty(v) = \frac{1}{2} \left[\tanh \left(\frac{v - v_1}{v_2} \right) + 1 \right] \quad (3)$$

$$w_\infty(v) = \frac{1}{2} \left[\tanh \left(\frac{v - v_3}{2v_4} \right) + 1 \right]. \quad (4)$$

When an oscillating system is moved adiabatically around in parameter space, returning to the initial point, the overall phase shift ϕ is made up of two components (Kagan, Kepler, and Epstein, 1991)¹: a *dynamic* time-dependent shift and a *geometric* time-independent shift. The dynamic shift is caused by the changing oscillator period during parameter variation, while the geometric shift is caused by the curvature of the surface enclosed by the path in parameter space. To recover the geometrical shift $\Delta\phi_{GPS}$, one can make use of its sign-reversal induced by changing the direction in which the parameter space is traversed (cf. Kagan, Kepler and Epstein, 1991):

$$\Delta\phi_{GPS} = \frac{1}{2}(\phi^\rightarrow - \phi^\leftarrow), \quad (5)$$

where ϕ^\rightarrow and ϕ^\leftarrow are the overall phase shifts obtained by, respectively, the clockwise and anti-clockwise traversals through parameter space. As the dynamic shift does not change sign with direction, subtraction of the overall phases results in the dynamic shifts cancelling out, while the geometric shifts (which do differ in sign) are summed.

To test for the existence of geometric phase shifts in the Morris-Lecar model, we varied two of its parameters $p_1, p_2 \in \mathcal{P}$ ($p_1 \neq p_2$) along an elliptical path (see Figure 1). The time at which the parameters start to be varied is denoted by t_i while the time at which they return to their original value is denoted by t_e . During the interval $t \in [t_i, t_e]$ the values of p_1 and p_2 are given by

$$p_1 = q_1 + r_1 \sin(2\pi\omega) \quad (6)$$

and

$$p_2 = q_2 - r_2 + r_2 \cos(2\pi\omega), \quad (7)$$

with $\omega = \frac{t-t_i}{t_e-t_i}$ ($\omega \in [0, 1]$) representing the fraction of the path traversed. The offset parameters q_1, q_2 and scaling parameters r_1, r_2 determine the minimal and maximal values of p_1 and p_2 along the path. Moreover, the scaling parameters provide control over the length of the path traversed through the parameter space.

Figure 1 illustrates the model we used to test for the geometric phase shift. Two Morris-Lecar neurons, denoted N^\rightarrow and N^\leftarrow in the figure, were simulated by numerically integrating the

¹In the non-adiabatic case there is a third component which decays to zero when the time to complete the path is increased.

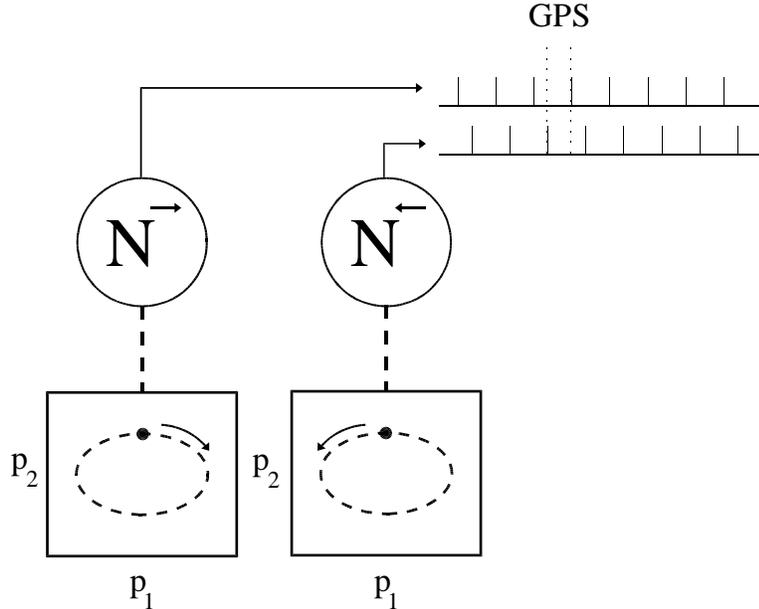


Figure 1: *Illustration of the model used to test for the geometric phase shift. The rectangular diagrams show the elliptical paths traversed through parameter space. The left diagram shows how two parameters of neuron N^{\rightarrow} change in a clockwise fashion. The right diagram shows the anti-clockwise path for the same parameters of neuron N^{\leftarrow} . The outputs of both neurons upon return to the original point in parameter space (filled dots in the diagrams) are illustrated at the top of the figure. The phase difference of the outputs is two times the geometric phase shift.*

equations (1), (6) and (7) using the fourth-order Runge-Kutta method (see, e.g., Press *et al.*, 1986). The parameter values were identical for both neurons with the exception of the r_1 radius parameter which was defined to have a different sign for both neurons, i.e., $r_1 = r$ for N^{\rightarrow} and $r_1 = -r$ for N^{\leftarrow} . With these parameter choices, the neurons traverse identical paths through parameter space in opposite directions. As a result, upon completion of the closed path, the presence and magnitude of a geometric phase shift should be visible in the presence and magnitude of a phase difference.

In our simulations we took the input variable i as our first parameter, with $q_1 = 0.11$ and $r_1 = 0.05$. As the second parameter we choose θ with $q_2 = 0.33$ and varied r_2 . The remaining nine parameters were kept at their default values (see the appendix). The choice of the offset and scaling parameters r_1, r_2, q_1 , and q_2 , were constrained to ensure that the oscillatory behaviour is maintained while the adiabatic path is traversed. To ensure that the path through parameter space is adiabatic, the time interval $t_{adiab} = t_e - t_i$, should be large.

3 Simulation Results

Figure 2 shows a number of snapshots of the limit cycles at evenly spaced values of ω for one of the neurons. While the parameter space is traversed, the shape of the limit cycle changes (as does the oscillator period), returning to its initial ($\omega = 0$) shape when the path is completed (at $\omega = 1$).

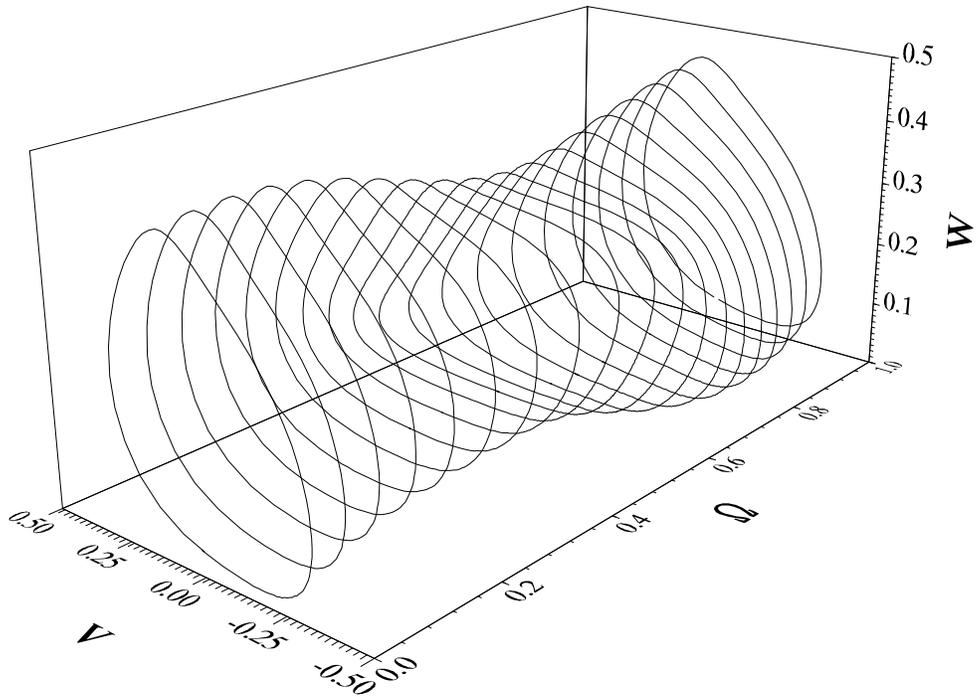


Figure 2: *Phase-plane ($v-w$) plots for the parameter trajectory at 19 evenly spaced values of $\omega \in [0, 1]$. Due to the cyclic path the phase-plane plots at $\omega = 0$ and $\omega = 1$ are identical.*

Figure 3 shows the geometric phase shift for several values of r_2 and $t_{adiab} = 10^8$ integration steps (stepsize = 0.05). Clearly, the Morris-Lecar model exhibits a geometric phase shift under adiabatic variation of its parameters i and θ . Within the shown range, the magnitude of the shift is a linear function of the area covered by the elliptical path. This linear dependence is consistent with the definition of the geometric phase shift as the integral of the path traversed in parameter space (Kepler and Kagan, 1991). For $t_{adiab} \leq 10^7$, this linearity is lost due to non-adiabatic effects.

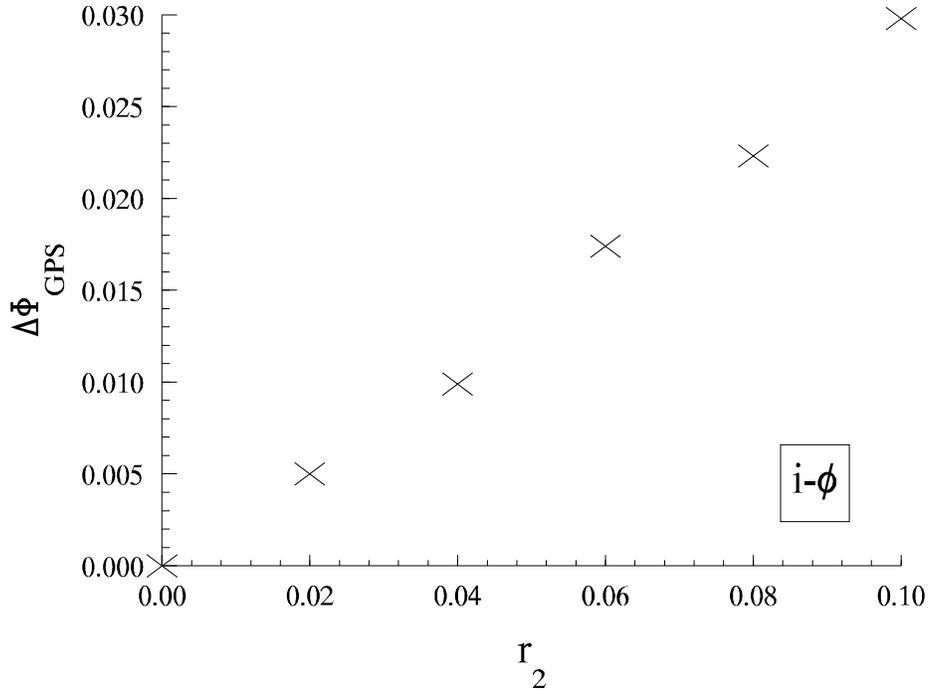


Figure 3: Geometric phase shift $\Delta\phi_{GPS}$ as a function of r_2 (which is proportional to the area enclosed by the elliptical path traversed through parameter space).

4 Discussion and Conclusion

The demonstration that a geometric phase shift can be induced in the Morris-Lecar model, indicates that this phenomenon may be functionally relevant for neural computation.² Broadly, the size of the shift may code the extent of an excursion from a state upon return to that state. Although, formally defined as a point in parameter space, a state may correspond to a condition internal to the organism, such as the concentration of a neuromodulating chemical. Variations in such concentrations, e.g., when their release is controlled by circadian rhythms, provide one example of where to look for the existence of functional geometric phase shifts in brain processes. In addition, the recent discovery of two-oscillator systems in the suprachiasmatic nucleus (Shinohara *et al.*, 1995) suggests that geometric phase shifts may even play a role in circadian rhythms themselves. Alternatively, the adiabatic path may (partly) result from cyclic

²In an attempt to demonstrate this functional relevance, we are currently studying geometric phase shifts in a simple phase-coupled neural network (Postma, van den Herik, and Hudson, 1996).

changes external to the organism. The variation of light intensity over the day, the rotation of the stars over night, and, departing from purely rhythmic phenomena, the movement of environmental landmarks induced by exploratory behaviour, all provide examples of such external variations.

We have provided some confirmation for Kagan *et al.*'s (1991) proposition that geometric phase shifts should be observable in biological systems by demonstrating their existence in the Morris-Lecar model. One of the roles of neural computational studies is to explain how known biological phenomena can achieve certain computational goals. Another role is to investigate what types of computation neural systems are capable of. In the former case, biology provides the problems and computational studies the solutions. In the latter, computational studies provide solutions which may direct biologists to go and look, as it were, for the problems. This study is one of the latter; a solution in search of a problem.

Appendix

The default values of the parameters used in the simulations are as follows: $v_1 = -0.01$, $v_2 = 0.15$, $v_3 = 0.1$, $v_4 = 0.145$, $g_{Ca} = 1.1$, $g_K = 2.0$, $g_L = 0.5$, $v_K = -0.7$, $v_L = -0.5$.

References

- Berry, M. (1988). The Geometric Phase. *Scientific American*, December, 26-32.
- Hopfield, J.J. (1995). Pattern recognition computation using action potential timing for stimulus presentation. *Nature*, 376, 33-36.
- Jefferys, J.G.R., Traub, R.D., and Whittington, M.A. (1996). Neuronal networks for induced '40 Hz' rhythms. *Trends in Neurosciences*, 19, 202-208.
- Kagan, M.L., Kepler, T.B., and Epstein, I.R. (1991). Geometric phase shifts in chemical oscillators. *Nature*, 349, 506-508.
- Kepler, T.B. and Kagan, M.L. (1991). Geometric phase shifts under adiabatic parameter changes in classical dissipative systems. *Physical Review Letters*, 66, 847-849.
- Llinás, R.R. (1988). The intrinsic electrophysiological properties of mammalian neurons: insights into central nervous system function. *Science*, 242, 1654-1646.
- Morris, C. and Lecar, H. (1981). Voltage oscillations in the barnacle giant muscle fiber. *Biophysics Journal*, 35, 193-213.
- O'Keefe, J. and Recce, M.L. (1993). Phase relationship between hippocampal place units and the EEG theta rhythm. *Hippocampus*, 3, 317-330.
- Postma, E.O., van den Herik, H.J., and Hudson, P.T.W. (1996). Computing with geometric

phase shifts. Manuscript in preparation.

Press, W.H., Flannery, B.P., Teukolsky, S.A., and Vetterling, W.T. (1986). *Numerical Recipes: The Art of Scientific Computing*. Cambridge: Cambridge University Press.

Rinzel, J. and Ermentrout, G.B. (1989). Analysis of Neural Excitability and Oscillations. In C.Koch and I. Segev (Eds.), *Methods in Neuronal Modeling. From Synapses to Networks*, pp. 135-169. Cambridge MA: MIT Press.

Shinohara, K., Honma, S., Katsuno, Y., Abe, H., and Honma, K. (1995). Two distinct oscillators in the rat suprachiasmatic nucleus *in vivo*. *Proceedings of the National Academy of Sciences, U.S.A.*, **92**, 7396-7400.

Singer, W. (1995). Time as coding space in neocortical processing: a hypothesis. In M.S. Gazzaniga (Ed.), *The Cognitive Neurosciences*, pp. 91-104. Cambridge MA: MIT Press.