Colin S Pittendrigh: An Appreciation

The Life of a Darwinian Clock-Watcher

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L Geetha studies circadian rhythms in honeybees, mice and humans.

A tribute to Colin S Pittendrigh, one of the three musketeers of chronobiology, who passed away on 20 March 1996.

It was fairly recently that I discovered CBT on the internet. CBT (Centre for Biological Timing), is an organisation that provides, among other things, information about research in the field of chronobiology. And so it was with great expectation of various kinds of interesting details about biological rhythms that I subscribed to it. It is my misfortune that the first piece of information that I received through CBT was that of the demise of one of the doyens of chronobiology, Colin S Pittendrigh. Nature could have been a little kinder to me. While I passed this sad news on to others in the field, it occurred to me that perhaps I should write a few words about him.

An introduction to the field of chronobiology to any student entails an introduction to the three musketeers, E Buenning, C Pittendrigh and J Aschoff. The first seminar that many students give is on one of the fascinating papers of Pittendrigh. It was thus, that I was introduced to him and the multitude of his research papers. Most of the intelligent experiments that have been conceived in this field were his brain work. At this moment, all of us are aware of the existence of rhythmic phenomena and we accept the presence of internal clocks. But this was not the case a few decades ago. Indeed, the attribution of the closing and opening of leaves in plants to the presence of an internal clock which measured external time, was often ridiculed. It required a lot of courage to speak up and prove to the world that clocks in fact exist and organisms exhibit rhythmic phenomena owing to the presence of internal biological clocks. Well, there were a handful

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of them who had this courage and their undaunting efforts to express themselves strongly has brought forth a slow transition from non-belief to belief !

Colin Stephenson Pittendrigh (1918 - 1996)

Pittendrigh's early research papers provided lucid explanations of the fundamental concepts of chronobiology such as entrainment and free-run. He, along with Aschoff introduced the 'oscillator language' to explain the mechanisms of entrainment and made innumerable predictions of how these overt behaviours by organisms could be the end product of the functioning of the internal oscillator. Pittendrigh also predicted that the clock should be sensitive to light and that this sensitivity should be different at different times of the day. To prove this, he constructed what is called the *phase response curve (PRC)* which describes the sensitivity of animals to light pulses at various phases. Pittendrigh describes the PRC poetically as the "footprint, as it were, of the pacemaker's (or oscillator or clock) time course"! He also demonstrated by an elegant set of experiments that the shifts in the phases caused by light pulses should be instantaneous. These experiments resulted in a series of four landmark papers along with S Daan in the *Journal of Comparative Physiology* (1976). The seeds of most modern experimentation are contained in these papers.

Pittendrigh had an open mind for new facts and was willing to change his views given sufficient experimental evidence. Thus, in his early experiments he talked about "the oscillator" inside biological systems and how "it" brings forth rhythmic expressions. Later, his own experiments on squirrels proved that there may be more than one oscillator which controls the activity rhythm of these animals. Thus he attempted to explain the occurrence of transients in the *Drosophila* system by a master oscillator and a slave oscillator. Now it is believed that multicellular organisms possess multiple oscillators, each controlling particular activities and still managing to remain in synchrony with each other. And according to Pittendrigh "it is a plausible and adequate

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interpretation for multicellular organisms".

The fruit fly *Drosophila* has now turned out to be a model system for most of the genetic and molecular work on clocks. Pittendrigh elevated *Drosophila* to a similar status in chronobiology. He demonstrated for the first time that biological clocks are temperature compensated i.e. clocks operate normally irrespective of the external temperature. Later, he proved such temperature compensation also in the unicellular *Euglena*. He extended it to *Neurospora*, and introduced it to the world "as a system in which the genetics of the clock could be pursued". Today, both *Neurospora* and *Drosophila* have indeed become powerful tools in the study of genetics of clocks. At this point of time, it has been established that the genes *per* in *Drosophila* and *frq* in *Neurospora* are responsible for the clock activities! They have been cloned, sequenced and exceptionally good progress has been made in deciphering the nature of their operation.

The greatness of a scientist lies not only in performing good experiments but also in reporting them to the world, in a convincing manner. Pittendrigh did this most effectively- each of his papers is a classic in itself. His research papers are written in such a simple, lucid and logical manner that even a beginner can feel proud that he understands them. I consider his "Reflections of a Darwinian Clock-Watcher" as his *magnum opus*, a brilliant, anecdotal article, written at the age of seventy five! It is a tragedy that he is no longer among us physically and it is indeed a great loss for the field of chronobiology! But the spirit of Colin Pittendrigh will live for ever and be rekindled by the writings of many generations of new students the world over.

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Suggested Reading

Hickory Dickory Dock.
T R Raghunand.
***Resonance* 4:76. April 1996.**

Stephen J Gould's view ... Contingency is rich and fascinating; it embodies an exquisite tension between the power of individuals to modify history and the intelligible limits set by laws of nature. The details of individual and species's lives are not mere frills, without power to shape the large-scale course of events, but particulars that can alter entire futures, profoundly and forever. (from *Eight Little Piggies*)