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Moonshine

Beliefs . . . in an influence of the moon on life on Earth . . . are by no means all moonshine.

H. Munro Fox, 1928

In 1957, Lamont C. Cole, a distinguished American ecologist, published an article entitled *Biological clock in the unicorn* (Cole, 1957). Surprisingly it appeared, not in a publication such as *The Annals of Improbable Research*, but in the prestigious scientific journal *Science*. It therefore had withstood critical scrutiny by peer review and was clearly of serious intent. In that journal, and with such a title, the article was guaranteed to make an impact, a precursor perhaps of scientific publications that in more recent years would compete for the Ig Nobel Prize for ‘science that makes you laugh and then makes you think’. The paper was published at a time when a group of his fellow American biologists headed by Frank A. Brown, Jr were describing daily rhythms of biological activity in a range of living things, from intact animals to slices of vegetables. From the running activity of rats on treadmills, to colour changes of fiddler crabs and oxygen uptake by slices of fresh potato, from locomotor activity rhythms in marine molluscs to oxygen consumption by marine algae, hourly values were shown to increase and decrease throughout the day in regular rhythmic patterns that persisted even in so-called constant conditions in the laboratory (Brown, 1954, 1958; Brown *et al.*, 1955a, b). On the basis of such findings, a heated scientific debate was taking place as to whether the rhythms were controlled by internal physiological processes (biological clocks) or by subtle environmental variables, such as solar and lunar day changes in the earth’s magnetic field and atmospheric pressure, and even daily fluctuations in the impacts of cosmic rays from space, that the experimental organisms in the laboratory were not shielded from. Brown and his co-workers favoured the view that daily changes in these residual geophysical variables could serve as time cues that triggered cyclical patterns of behaviour in living things and Cole's paper sought to present an unsubtle challenge to that view.

Brown (1965) presented a strong rebuttal of the Cole paper, referring to it as an 'unfortunate, very misleading publication'. He stated that the first studies of his group were based on the classical assumption that rhythmic periodicity was timed independently within each organism, as in Brown (1954) and Brown *et al.*, (1955a, b). For example, they reported persistent, seemingly internally generated, that is endogenous, daily and tidal rhythms of oxygen consumption in fiddler crabs. However, they quickly reasoned that if such rhythms were truly endogenous their patterns should vary significantly with temperature, which was found not to be the case (Brown *et al.*, 1954). This seemed most unexpected if biological timing was achieved by an internal physiological process so, one year after publication of the Cole paper, Brown (1958) again argued against the existence of internal biological clockwork. He claimed that he had 'incontrovertible evidence that even when we have thought we have excluded all forces influencing living things, there is, nonetheless, cyclic information, unquestionably with all the natural periodicities of the atmosphere imbedded in it, still impressing itself upon the organism'. Later, Brown (1962a, b) still considered that there was no evidence available to suggest that organisms possess independent timing mechanisms, but that they are 'dependent for their timing upon continuing response to the subtle rhythmic geophysical environment', referring to 'extrinsic rhythmicality' as a 'reference frame for biological rhythms under so-called constant conditions'. Brown and his co-workers therefore challenged the views of many other biologists at that time who were coming to accept the idea of endogenous clock-controlled biological rhythms. Brown's proposal was provocative, but the notion that animals, and even plants, possess some form of internal time sense had been in favour for much longer.

The French astronomer Jean Jacques de Mairan, early in the eighteenth century, incisively noted that the daily opening and closing of the leaves of *Mimosa* continued for several days in a nearly normal manner, even when plants were kept away from daylight cues in a continuously darkened cellar (see Daan, 1982). Later in that century Henri-Louis Duhamel du Monceau successfully repeated the experiment, keeping temperature constant, too, by observing his plants in a wine cave (see Winfree, 1987). His, and other, early interpretations as to how such rhythms were controlled considered that plants and animals learned, during their lifetime, to perform rhythmic behaviour that matched cyclical changes in their environment. Organisms were thought to establish daily patterns of behaviour in response to the benefits obtained by reacting in a particular way at one stage of the day/night cycle but not at another. That interpretation was strongly supported early in the twentieth century and, by the mid-twentieth century, it was extrapolated by some authors to suggest that time-keeping ability could be an inherited characteristic of living organisms.

Interestingly, this now fairly generally accepted view is contrary to that of Charles Darwin (Darwin and Darwin, 1880) himself, who had earlier questioned how rhythmic behaviour could have arisen by natural selection. He was particularly concerned as to how to explain the daily pattern of leaf opening and closing behaviour in plants. In fact, it remains the case for many animals and plants, that the selective advantage of innate rhythmicity has yet to be demonstrated experimentally. However obvious it may appear to be, it is difficult to prove that organisms with supposed inbuilt clockwork have a greater potential for survival over evolutionary time than individuals of the same species without such a timing mechanism, a point which will be discussed later.

It was perhaps because of uncertainties concerning how natural selection could favour inherited biological clocks that Brown (1958, 1960, 1962a, b, 1965) refocussed the debate, arguing that proponents of the internal biological clock hypothesis had not carried out sufficiently rigorous experiments. Even in 'constant conditions' in the laboratory, which usually meant controlled light, temperature, humidity and, for coastal animals, an absence of the influence of tides, living things, he argued, would still be exposed to some environmental variables that were not kept constant. He therefore concluded that organisms in such conditions were in fact responding to residual geophysical variables and were not behaving in response to their genetic makeup. Brown's interpretation persisted in some quarters, despite crucial evidence to the contrary that had been obtained even as early as the nineteenth century. Indeed, some of his more provocative findings were still being quoted as fact on the Internet in the early twenty-first century, despite serious questioning of their validity in the scientific literature after they were first published (see Chapter 5).

In the early 1800s, following up the earlier experiments by de Mairan and du Monceau, further studies of the leaf-opening rhythm of *Mimosa* were carried out in Geneva by Augustin Pyramus de Candolle. He found that in continuous dim light the plants exhibited not a 24-h rhythm of leaf opening and closure, but one of 22 to 22.5-h periodicity (see Winfree, 1987). Then, a century later, in the 1920s, similar evidence emerged concerning the behaviour of another plant, *Canavalia*. The periodicities of 'daily' rhythms of leaf movements of this plant in constant light, like those of *Mimosa*, were shown by Anthonia Kleinhoonte in Holland to deviate slightly from 24 h, at periods quite different from any known subtle geophysical variable that might be considered as a candidate to drive such rhythms in normal constant environment rooms in the laboratory (Kleinhoonte, 1928). Evidence such as this fostered scepticism of Brown's interpretation in the 1950s to the extent that Cole (1957) was prompted to test directly the hypothesis that biological rhythms might occur, not only in the absence of the more obvious environmental variables, but also when an animal was deprived of exposure to subtle geophysical variables too. Accordingly he elected to search for biological rhythms in an animal that could not possibly be influenced by such earthly factors, the mythical unicorn being ideal for his purpose.

Since Brown and his co-workers had demonstrated patterns of daily variation in the metabolic rate of, for example, potatoes, seaweed, carrots, earthworms and newts, the first task for Cole was to acquire data on the metabolism of his mythical animal. To do this he took a sequence of 120 values from a table of random numbers and postulated that they were consecutive hourly values of the standard metabolic rate of a unicorn kept for five days completely isolated from cycles of environmental variability, as of course they usually are. All that was then required for Cole was to use Brown's methods of statistical analysis of the time-series of its 'oxygen consumption' data to show whether or not the unicorn exhibited repeated daily changes in metabolism during its five days of sensory deprivation. Amazingly, from this analysis, the mythical unicorn did appear to show a consistent daily pattern of metabolic activity; its metabolism was greatest at night and least in the afternoon!

The point of the story lies in the fact that Cole used Brown's method of analysis of sequences of hourly values of biological data. Time series analysis of sequential data in the twenty-first century is now more sophisticated and objective but, in the 1950s, some procedures evidently succeeded in generating apparently meaningful biological rhythms, even in random data (see Enright, 1965a). The problem arose because Brown used data manipulation procedures that involved packaging sequential values of oxygen consumption into various sub-sets that could then be pooled for mathematical analysis. In his search for biological responses to residual geophysical variables, the challenge for Brown was to distinguish the responses of an organism to two daily patterns of change in these small scale changes that are of similar periodicity. These are of 24-h (solar day) periodicity, associated with the earth's rotation in relation to the sun, and of 24.8-h (lunar day) periodicity associated with the perceived rotation of the earth in relation to the moon. Packaging of hourly data values to search for lunar day rhythms involved 'data-slipping', which was considered by Cole to be a major factor in generating apparent rhythmicity in random data. In his publication Cole (1957) was clearly questioning the validity of the concept of biorhythms linked to residual periodic variables, and also issuing a challenge to chronobiologists to use more rigorous statistical methods when seeking to demonstrate rhythmic phenomena in plants and animals.

Whilst it is known, for example, that some animals appear to orientate to the pattern of the earth's magnetic field when navigating over long distances (see Chapter 5), no direct evidence has yet emerged to support the view that cyclical changes in the energy fields of residual geophysical variables are detected and used solely by organisms as external (exogenous) daily time cues such as to preclude recognition of the existence of internal biological clocks. Nevertheless, the old controversy about whether biological rhythms are driven by endogenous or exogenous factors was later re-opened by Martin and Martin (1987). These authors raised the possibility that the 24-h behavioural rhythmicity of honeybees is not controlled by an endogenous, that is circadian, clock, but is controlled solely by exogenous factors. Specifically, it was proposed that bees respond to diel changes in the geomagnetic field and do not possess internal biological clocks. That interpretation was challenged immediately by Brady (1987), starting from the premise that most workers in the field of chronobiology must have thought the debate long since settled. Brady re-examined the data of Martin and Martin concluding that they were consistent with the more generally accepted explanation of endogenous circadian rhythmicity, though acknowledging the probability that bees do use local magnetic cues to set their feeding rhythms (see also Chapter 10). Certainly, in recent decades, a plethora of examples among plants and animals has emerged to confirm the endogenous nature of many rhythmic biological phenomena, which free-run at periodicities that only approximate to environmental cycles when deprived of such cues in the laboratory. In fact, since the mid-twentieth century, research on the nature of biological rhythms has proceeded by seeking answers to the following questions:

1. Do organisms in general show behavioural and physiological rhythms when maintained in constant conditions?
2. What are the properties of such rhythms and how persistent are they?

3. What and where is the physiological clock which controls the approximate periodicity of the rhythms being investigated?
4. What is the role of environmental variables and how, in nature, do they effect accurate phasing of endogenous physiological clocks?
5. What is the ecological significance and, hence, the adaptive value of rhythmic behaviour and physiology in animals and plants?

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The concept of the 24-h biological clock is now in common usage, as recognition of the phenomenon of jet-lag in air travel confirms. Humans carry a body clock as they move around the earth and sense that resetting the clock in a new locality takes a longer or shorter time depending on the longitudinal distance travelled. Indeed, it can be said that the concept of the human body clock can be confirmed by experiment since by ingesting medicinal melatonin the clock resetting process can be speeded up. A physiological basis for such clockwork has been demonstrated in many animals including humans, clockwork which when deprived of external time cues is expressed as circadian rhythms of sleep/waking and various bodily functions. The word ‘circadian’ is also in general acceptance and quite common usage now; it defines rhythms of periodicities that approximate to the 24-h day and which are expressed in the absence of the external, clock-setting environmental cycles. The nature of circadian rhythms is best understood if the word circadian is pronounced *circa-dian* (literally: approximately daily) and not *cir-cay-dian*, which is most commonly the case.

It is, then, easy to believe that many living organisms on the spinning earth possess their own internal biological clocks (see also Dunlap *et al*., 2004). General acceptance is such that the subject once attracted over-optimistic interest from stock market speculators and others seeking to prosper from the new science of ‘Chronobiology’. In the early days of biorhythm conferences, speculative funding support came from financiers anxious to find out if economic cycles and trends in stocks and share values could be predicted by the new science. The only reasonable prediction was that the funding source would dry up quite quickly when it became apparent that chronobiologists had little to offer stock market speculators in exchange for conference-funding support. Other speculators, however, did succeed in marketing charts, books and even pocket calculating machines extolling what came to be known as the ‘Biorhythm Theory’. The theory was based on suppositions that found their way into the medical literature that human physical ability waxes and wanes every 23 days, emotional condition varies on a 28-day cycle and intellectual performance follows a weak 33-day cycle. It was taken sufficiently seriously in the 1970s to be put to the test by airlines, the military and the insurance industry, all anxious to know if there was anything in it for them. Not surprisingly, perhaps, in all cases the theory was found to be wanting, leading Winfree (1987) to point out, that 'Biorhythm Theory' is no more than pseudoscience, with no justification whatsoever. Biorhythm Theory is to chronobiology what astrology is to astronomy, and it has done nothing to advance the credibility of the science of biorhythmicity. By contrast, chronobiology impacts significantly on medical research into sleep and other human rhythms, and on medical chronotherapeutics, which is concerned with the optimization of times of application of drugs (Winfree, 1987).

So, the strength and repeatability of daily changes in solar illumination can reasonably be assumed to have provided, over geological timescales, a suitable environmental backdrop against which circadian clocks have evolved, not only in humans, but also in a wide range of animals and plants. Indeed, the subject has wide implications for the exploitation and management of the world's natural resources. Sustainable exploitation in agriculture and fisheries, optimization of conditions for artificial cultivation of living organisms, and the development of rational strategies for environmental conservation, should all be founded on a full understanding of the cyclical nature of living animals, plants and ecosystems (Naylor, 2005). Is it the case then that the repeatability of lunar cycles, like that of solar cycles, has also provided a consistent environmental background against which tidal time-keeping ability has been selected for during the timescale of biological evolution? Certainly, many biologists, before and after Cole, have expressed reservations about moon-related activities in animals. However, direct responses to moonlight, particularly in relation to the lunar monthly cycle, but possibly also in relation to the lunar day, may not be so far-fetched as is sometimes assumed, as will be discussed in Chapter 5. Moreover, indirect effects of the moon reflected in the tidally related behaviour patterns of marine animals are now well understood and it is the nature of ocean tides which provide the evolutionary backdrop to those behaviour patterns that will now be considered.

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Ocean tides on earth are caused primarily by the gravitational pull of the moon, and to a somewhat lesser extent by the gravitational effect of the sun (see Pugh, 1987) and they vary according to the moon's orbit around the earth and the combined earth–moon orbit around the sun (Figure 1.1; Plate 1). The moon's gravitational force draws up a bulge in the sea lying beneath it, which is balanced by a reciprocal, centrifugally

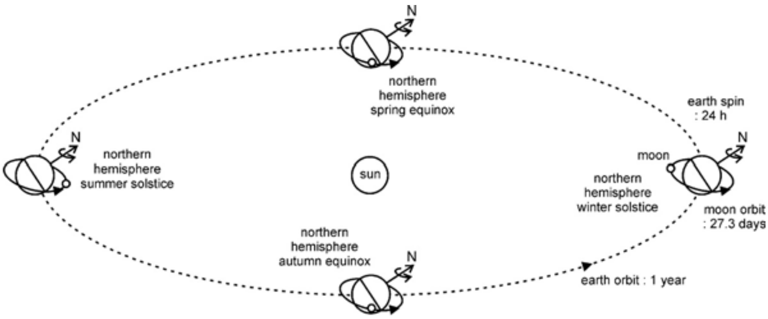

Figure 1.1 Earth tilt and spin, tilted orbit of the moon, and earth–moon orbit around the sun.

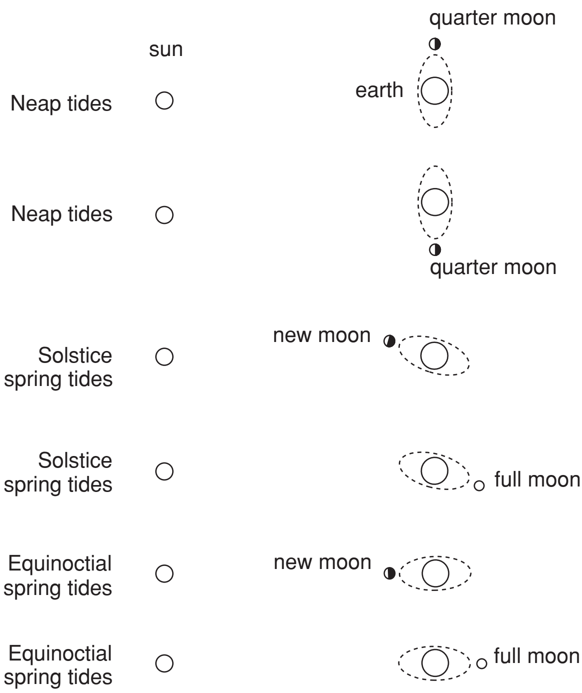

Figure 1.2 Snapshots of relative positions of the moon and sun that generate neap tides, solstice spring tides and equinoctial spring tides, showing exaggerated tidal bulge (dotted) in each case.

generated bulge in the sea on the opposite side of the earth (Figure 1.2). The centrifugal force that generates the reciprocal bulge arises because the earth and the moon are effectively spinning as one mass, the common centre of gravity of which is not the centre of the earth but a point nearer the earth's surface in the direction of the moon. Since the distortion of the ocean remains stationary in relation to the moon, the daily

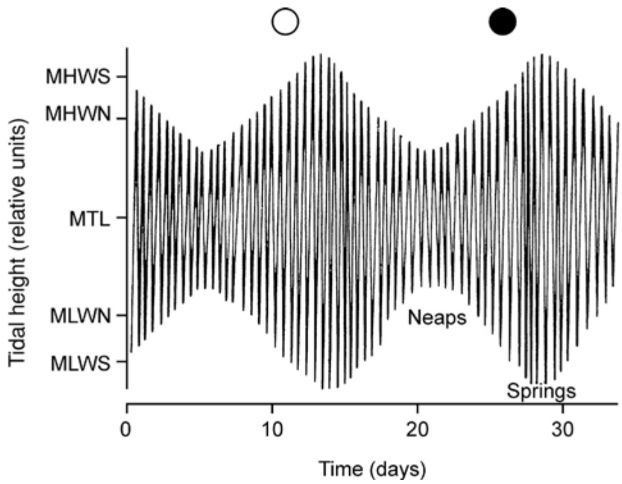

Figure 1.3 Generalized pattern of semidiurnal tides (12.4 h intervals) over a lunar month. MHWS, mean high water spring tide level; MHWN, mean high water neap tide level; MTL, mid tide level; MLWN, mean low water neap tide level; MLWS, mean low water spring tide level; open circle, full moon; closed circle, new moon (after Naylor, 1982).

rotation of the earth ensures that an upward bulge in the sea, that is a high tide, appears at any one point on the earth's surface twice every day. If the moon was stationary above the earth the interval between successive bulging high tides would be precisely 12 h, as a function of the 24-h rotation of the earth. But, of course, the moon itself is also moving, on its monthly orbit around the earth. This displacement, together with the daily rotation of the earth gives to an observer at any point on the earth an apparent orbit of the moon around the earth of 24.8 h. This defines the lunar day, as distinct from the 24 h solar day. So, with a lunar day of 24.8 h, and two ocean bulges typically passing during that time, the condition of high tide is generated at any one point on earth every 12.4 h, that is twice every lunar day, defined as semidiurnal tides (Figure 1.3). Such tides would be readily predictable from the position of the moon overhead if the earth was completely covered by an ocean of uniform depth, if the orbit of the moon was exactly in the plane of the earth's equator, if the plane of the earth's equator was exactly in the plane of the earth's orbit around the sun, and if other things were equal; but none of these requirements prevails.

First it is important to note that the orbit of the moon is tilted in relation to the earth's equator. Twice during each of its monthly (27.3 day) orbits around the earth the moon passes over the equator but, between times, the declination of its orbit is such that it is directly overhead in the northern hemisphere during part of its orbit and, about 14 days later, is overhead for several days in the southern hemisphere. As a result, the tidal bulge beneath the moon, and its reciprocal on the other side of the earth, oscillate northwards and southwards of the equator throughout the lunar month. This gigantic oscillation means that in some latitudes and at certain times of a lunar month, a particular locality on the spinning earth will be exposed to the deep part of one tidal bulge and to a shallow part of the opposite bulge 12.4 h later. Consequently, such localities experience more-or-less equal semidiurnal tides at those times of the month when the tidal bulges align with the equator and, at other times, alternate tides will be somewhat different in height. Geographical regions of the earth that experience such alternating patterns of tidal oscillations are said to experience mixed semidiurnal tides. Indeed, in some localities the inequalities may be so extreme as to produce only one high tide every 24.8 h.

Other factors, too, further complicate the tidal picture. Continental and island land masses interrupt water flows as the tidal bulges pass, and lateral flows may be exaggerated depending upon inshore depth and coastline shape, particularly along straits and estuaries. In addition, Coriolis force, generated by the rotation of the earth, deflects water movement to the right in the northern hemisphere and to the left in the southern hemisphere, generating local differences in the timing of high tide.

Also, strikingly in many localities, there are lunar monthly variations in the height of high tides. These are well known to fishermen and small boat owners who, if forgetful, may for several days on two occasions each month, find their craft high and dry, that is neaped, above high tide. To understand these monthly changes in tidal height it is necessary to consider not just the interaction of the earth and moon on a daily basis, but also their relationship to each other and to the sun over the lunar month. It is also necessary to take into account the additional gravitational effect of the sun on ocean tides and, therefore, the combined effects of lunar and solar gravity. Though the sun is vastly larger than the moon, it is so far away that its gravitational effect on earth ocean tides is only about half (46%) of that of the moon, but it nevertheless has a significant impact.

The time taken for the moon to orbit the earth, 27.3 days, is defined as one sidereal month. After that time, the moon returns to the same point overhead relative to the earth. However, because the earth and the moon together have also moved during this time in their orbit around the sun, the moon does not regain its position on the line between the earth