A Sun compass in monarch butterflies

Each autumn, monarch butterflies (*Danaus plexippus*) migrate up to 4,000 km from breeding grounds in the eastern United States and Canada to overwintering sites in Mexico[1,2]. We tested the ability of monarchs to orient using a Sun compass by clock-shifting[3] the butterflies and observing the orientation of their subsequent flight. Clock-shifted migrants reoriented their bodies in the predicted clockwise direction whereas control groups of migrants did not. This indicates that monarch butterflies are able to orient during their transcontinental migration using a Sun compass.

In conjunction with a knowledge of the time of day, many animals are able to use the Sun's changing azimuth to orient their migratory and homeward movements[4]. Beginning with Schmidt-Koenig[3], Sun compass use has been demonstrated by clock-shifting experiments. A change in the internal clock causes animals to misinterpret the position of the Sun, and hence change their direction of movement in a predictable way. In the Northern Hemisphere, for example, time-delayed migrants exhibit a clockwise change in orientation.

During September 1996, in eastern Kansas, we experimentally clock-shifted (delayed) migrating monarchs by six hours to determine whether these butterflies use a time-compensated Sun compass. We released clock-shifted subjects individually and watched them for 1–5 min. We ran behind and beneath butterflies to estimate body orientations (headings) maintained for 15 s or more, using hand-held compasses. Migrants that were kept in the laboratory but not clock-shifted served as a sham control group and naturally migrating butterflies served as 'natural' controls.

The mean heading for clock-shifted butterflies was toward the west-northwest (Fig. 1a), which is 75° from the mean south-southwest orientation of the sham controls (Watson's F-test, $F = 13.84$, $P < 0.01$; Fig. 1b) and 85° from the mean natural control measure ($F = 49.02$, $P < 0.01$; Fig. 1c). The mean heading of the clock-shifted butterflies bears out the clockwise change in direction predicted by the clock-shift delay experienced, and is of the magnitude predicted by the 6-hour time shift. Importantly, the two control groups exhibited strikingly similar mean headings ($F = 1.93$, $P > 0.05$), indicating that there was no significant effect of captivity.

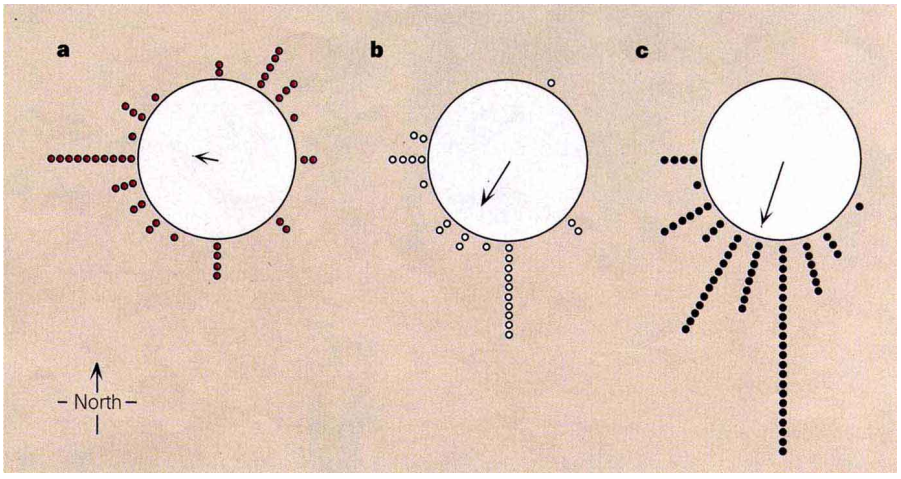

Figure 1 **Mean body orientation data, giving resultant vector direction (μ) and length (r) for** a, **clock-shifted migrants ($\mu = 287°$; $r = 0.29$; $n = 43$, each circle represents 1 migrant);** b, **sham controls ($\mu = 211°$; $r = 0.67$; $n = 25$, each circle represents 1 control); and** c, **natural controls ($\mu = 200°$; $r = 0.86$; $n = 204$, each circle represents 3 controls). Subjects not exhibiting directional flight for any reason (for example, spiralling upwards on thermal currents, stopping to feed) were excluded from the analyses. Of 532 migrants observed, 272 yielded stable heading data.**

Monarch butterflies in North America use a Sun compass during their southward autumn migration, orienting their bodies using the time of day and the position of the Sun. The monarch butterfly thus joins the small group of species for which a Sun compass orientation mechanism has been demonstrated experimentally. In the absence of celestial cues on overcast days, however, monarchs still manage to orient towards the south-southwest[5], suggesting that they also have a non-celestial backup mechanism of orientation, such as a geomagnetic compass[6,7].

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Electrical recording from a glass sponge

Sponges arose very early in metazoan evolution. They do not have a nervous system, but some respond to stimulation by producing local contractions and one group, the 'glass sponges' (Hexactinellida), shows coordinated arrests of movements of the flagella, which produce the feeding current[1,2]. We show here that these arrests are coordinated by propagated electrical impulses. This is, to our knowledge, the first report of electrical signalling in any sponge.

Previous attempts to record electrical activity from sponges have been hampered by the delicate, porous nature of the tissues, which makes attachment or insertion of electrodes difficult. In the sponge that we studied (*Rhabdocalyptus dawsoni*) the tissues are very flimsy, consisting of thin, perforated sheets and filamentous strands draped around a scaffold of spicules, like a three-dimensional cobweb[3]. Few of the strands exceed 20 μm in thickness and the surface layers are about 1 μm thick.

To record from the sponge we dissociated tissue and allowed it to aggregate, using Concanavalin A to promote adhesion[4,5]. When the aggregates had rounded off, we placed them on the surface of slabs of body wall taken from the original sponge. After 12 h the grafts were attached and after 24 h cytoplasm could be seen streaming into the sponge (Fig. 1a). The tissue formed a substantial lump to which suction electrodes could be attached (Fig. 1b).

After 24 h, we put the slabs into a perfusion chamber in a shielded recording cage, inserted stimulating electrodes and positioned a thermistor-bead flow meter over the preparation to record changes in water flow across the body wall. We then attached

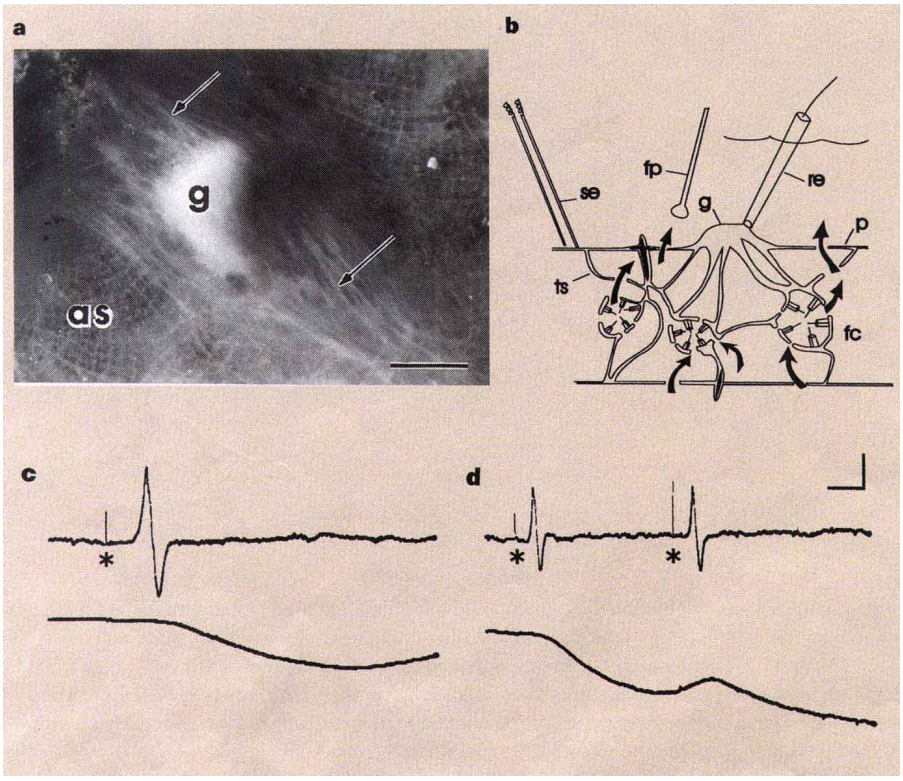

Figure 1 a, **An attached graft (g) 24 h after being placed in contact with the atrial surface (as) of a piece of sponge. Arrows show streams of cytoplasm passing from the graft into the sponge. Scale bar, 1 mm.** b, **Diagram of a section through the body wall of *Rhabdocalyptus* showing a graft (g) fused to the pinacoderm (surface layer, p) of a piece of sponge. re, suction recording electrode; ts, trabecular syncytium; fc, flagellated chambers; arrows, water flow across the body wall; fp, probe to detect changes in flow velocity; se, chlorided silver stimulating electrodes.** c,d, **Recordings from such a preparation. Upper traces, electrical records from the suction electrode; lower traces, changes in water flow velocity past the flow-meter probe. Shocks (shown by asterisks) were delivered at a point 1.1 cm from the recording point. In** c **a single shock evoked a propagated action potential followed immediately by a reduction in water flow velocity. In** d, **a second shock delivered 40 s after the first evoked a second impulse and a more complete arrest of the feeding current. Time scale: 5 s in** c, **10 s in** d. **Voltage scale (upper trace), 0.1 mV.**

a polyethylene suction electrode (internal diameter 80 μm) to the graft, close to the flow probe. We stimulated the preparation with single electrical shocks, delivered more than 1.0 cm from the recording point, and displayed changes in water flow and associated electrical events, recorded through capacity-coupled amplifiers (0.1 Hz time constant), on an oscilloscope.

We consistently recorded an electrical impulse preceding each arrest of the feeding current (Fig. 1c). Amplitudes lay in the range 50–200 μV depending on the suction applied to the recording electrode. The signal was lost if the suction was insufficient to produce a good seal. Conduction velocities lay within the range of values previously reported for the spread of arrests (0.17–0.3 cm s^{-1} at 11 °C)[1]. After an impulse, the preparation was refractory for 30–40 s. A second shock 40 s after the first evoked an impulse identical to the first, with summing of the effector responses (Fig. 1d). Impulses were initially positive-going, showing a simple biphasic form and a duration of ~5.0 s.

We suggest that the tissue responsible for the conduction of the electrical activity is the trabecular syncytium, which makes up 75% of the organic matter in the sponge. This system penetrates all parts of the sponge, including the flagellated chambers where the effector response takes place. The syncytial character of this tissue, first reported using light microscopy, has now been confirmed by electron microscopy[3] and *in vitro* studies[4,5]. Aggregates are also syncytial[6] and fuse with the trabecular syncytium when placed in contact with it. The absence of membrane barriers within the syncytium presumably allows action currents to spread in any direction from sites of depolarization. Thus, there is a clear path for the propagation of impulses through into the graft.

As yet, we do not know the ionic basis of the action potential, and although channels have never been identified in sponges[7] we assume that voltage-activated channels are involved, as in other excitable tissues. Our findings place *Rhabdocalyptus* firmly on the list of animals capable of non-nervous conduction[8] and strengthen the view that excitability arose in the metazoa before the evolution of nerves.

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Inferring seal populations from lake sediments

An explosion in the population of Antarctic fur seals (*Arctocephalus gazella*) has caused widespread changes to many coastal terrestrial and freshwater ecosystems in the northern maritime Antarctic islands and on the west coast of the Antarctic Peninsula. We have used seal hairs found in lake sediment cores from one maritime Antarctic island as a historical record of seal populations. This has enabled us to examine possible causes of the increasing numbers of visiting Antarctic fur seals, and has provided a historical framework from which to evaluate conservation plans to minimize the adverse effects of seals at sites of particular ecological significance.

Although hunted to near extinction during the nineteenth and early twentieth century, the numbers of Antarctic fur seals have recently been increasing[1,2]. On Signy Island in the South Orkney Islands, the number of seals visiting each summer from the main breeding beaches on South Georgia has increased from less than 100 before 1976 to almost 20,500 in 1994 (ref. 2). This large increase has caused extensive destruction of vegetation, soil erosion and the eutrophication of freshwater lakes on coastlines where the seals haul out[2–6].

The Protocol on Environmental Protection was adopted by the Antarctic Treaty Nations in 1991 and it is expected to enter into full international force in the near future. Given the commitment of the Treaty Nations to limit adverse impacts on Antarctica, the current Antarctic fur seal population explosion raises three questions. First, is the increase a result of human or natural influences? Second, does the increase exceed the range of normal population variability during the past several thousand years? Third, how might any control measures that are deemed necessary be best implemented