

General biology

The Red-spotted Newt *Notophthalmus viridescens* is a semi-aquatic species which as an **adult** spends most of its time in the breeding/home pond but may straggle around within a few kilometer spending its time on land or in water. Animals away from the home pond at certain times of the year migrates back to the home pond. In the juvenile years (in the so called eft-stage) the newt is found mostly on land. All experiments were performed with adult newts.

Fischer et al. (2001, p.2) is a good entrance. "(1) *Adult eastern red-spotted newts in many populations are migratory, leaving the water seasonally to avoid temperature extremes and migrating back into ponds at the beginning of the breeding season (Hulbert 1969; Gill 1978, 1979).* (2) *Displacement experiments have demonstrated that a majority of adult male newts home back to the pond from which they were captured at the onset of the breeding season (Gill 1979). At these times of year adult male newts held under controlled laboratory conditions switch from shoreward compass orientation to homing orientation relative to the direction of the magnetic field (Phillips 1987; Phillips & Borland 1994)*".

Clearly, the Red-spotted Newt seems to be a very unlike candidate for making use of **magnetic gradient navigation** when migrating towards the home pond, whereas a **magnetic compass** sense seems to be a reasonable possibility.

General procedure

Newts were taken from the breeding/home pond and transported far away (10 – 40 km) to a laboratory/(tank/testing) area.

Here the newts were placed in outdoor all glass aquarias (water-tanks), 120 l (90 times 30 times 45 cm) with an artificial shore in one of the long ends, which could be directed towards N, E or W (never S). The newts spend several days/weeks in these outdoor water-tanks. The water in the tanks was temperature-regulated and two different treatments were used to bring the newts into motivational states for displaying **shoreward** directed orientation or **homeward** directed orientation.

The newts were tested indoors on land on a horizontal circular disc under artificial illumination from above under one of four magnetic alignments: 1) in the natural magnetic field (i.e. $mN = N$) or in artificial fields (resembling the natural field in intensity and inclination) where magnetic N was directed towards 2) S, 3) E or 4) W ("*the rotated fields closely resembled the ambient field in inclination (+/-1-2°) and total intensity (+/-5%)*"). In general (according to their behaviour after the release on the disc) only half of the newts were accepted for showing significant orientation.

The orientation of the (accepted) newts from a given sample were then denoted in reference to magnetic N, or transferred in reference to the shore-direction and/or the home-direction.

The results, short about the papers

P (1987) is the basic paper, where the newts from home-ponds towards the directions of SSW or ESE were tested after staying in N/S-directed outdoor water tanks: In a **first series** without special temperature treatment but in 1) the natural season for homeward migration or 2) outside this season.

In these experiments there was no shore in the tanks. During “*January – March weak bimodal magnetic orientation (was found) along the axis of the holding tank*”. “*During the spring migratory period (April until early May) the bimodal response shifted to coincide with the direction of the pond from which the newts had been collected*”. In a **second series** the water temperature was regulated for motivating shoreward or homeward orientation, respectively. Here the N-end of the tank was made as a shore. Now – according to treatment – unimodal orientation was seen in both shoreward orientation and in homeward orientation.

Obviously for P an appropriate temperature treatment influences the motivation for homing (or shoreward orientation) and changes a weakly motivated, bimodal response into a strongly motivated, unimodal response.

It is not discussed whether there is a connection between shoreward and homeward orientation, nor whether the application of a shore in one end in the water tank (second series) could be responsible to the change from bimodal into unimodal orientation.

P (1986, J. Comp. Physiol.) connects closely to the preceding paper and P concludes “*in an earlier study, newts tested without exposure to elevated water temperature exhibited weak bimodal magnetic orientation. This bimodal response varied seasonally. During the winter months, the newts exhibited a trained compass response. However, at the onset of the Spring migration (April – early May in the Ithaca area), they switched to orienting along an axis coinciding with the direction of the pond in which each group was collected*”.

Following appropriate temperature treatments **shoreward** orientation towards N was demonstrated for populations from both SSW and ESE, as also shoreward orientation towards about E for the eastern population.

P (1986, Science) Newts from home ponds about 20 km E-ESE of the laboratory displayed **shoreward** orientation established in reference to a magnetic inclination compass – as inversion of the inclination (without changing the polarity) in the test-phase leads to an orientation shifted about 180°. On the other hand, the **homeward** orientation is unaffected by the inversion and this leads P to the obvious conclusion that the newts for navigation make use of a compass steered by the polarity of the magnetic vector – with the words of P “*a distinct magnetoreception pathway with polar response properties is involved in homing and is possibly linked in some way to the navigational map*”.

The comments of mine should be that the navigational map needs (integration with) a compass and this compass is a polarity compass if the gradients are based in the magnetic field. When the homeward orientation is unaffected this also means that there is no transference from the polarity compass to an inclination/axial compass in the test-phase – and this observation/conclusion is interesting in reference to some of the experiments presented in the next papers, where the wave-lengths of the light is changed in the tank- and/or in the test-phase.

P&B (1992, Anim.Beh.) Populations taken from home-ponds 10 to 60 km away from the laboratory and treated and tested for **shoreward** orientation in near-infra red light (>715 nm) were disoriented, whereas the controls were shoreward oriented. However, perhaps – not remarked by P&B – the orientation was bimodal about perpendicular to the shore direction (I calculated a sample mean vector of 240°/60° - 0.241 (n = 22) if doubling the angles, compared with 277° - 0.11 if not doubling the angles).

P&B (1992, Ethol Ecol & Evol) As in the preceding paper the newts were kept in the tanks exposed for the full spectrum light, but then – after temperature treatment for **shoreward**

orientation – tested under conditions of 1) full, 2) short waves (450 nm), or 3) long waves (550 nm).

The orientation was shoreward in 1) and 2), but about 90° counterclockwise (CCW) in 3) (not quite statistically significant).

The following (p.40) is worth citing (bold letters are mine) “*Previous experiments have shown that newts will shift from shoreward to **waterward** orientation (i.e., a 180° shift in direction) **in response to a variety of environmental factors** which influence their physiological state (Phillips 1987a, and unpubl.observ.)*”. However, P 1987a says nothing about waterward orientation.

This is interesting and together with the reactions under different wave-lengths indicates a basic **cross-axis system**.

P&B (1992, Nature) as the preceding papers is about **shoreward** orientation only. After exposure to full light in the tanks the newts were tested 1) 400 – 450 nm, 2) 475 nm, or 3) 500, 550, 600 nm. The orientation was shoreward in 1), random in 2) (according to P&B. However, doubling the angles improved the concentration and a bimodal observation at right angles to shoreward) was rather obvious (80°/260° - 0.26, n = 17). 3) about 90° CCW.

If trained in tanks under long waves there was shoreward orientation if tested under longwaves, but 90° CW if tested under full light.

P&B (1994) In this paper is shown that the **wave-lengths** of light in the **test phase** also has an influence on the **homeward** orientation. After **exposed for the full spectrum in the tanks** the newts were tested under 1) full, 2) short (400-450 nm) and 3) long waves (550, 600 nm). The newts were homeward oriented in 1) and 2) but random in 3).

Much talking and a dubious model for an interaction between the two different compasses followed.

P&B (1995). “ - - newts - - deprived of directional information during long distance displacement from their home pond were able to orient in the homeward direction, indicating that they are capable of true navigation”.

The newts were “ - - deprived of visual, magnetic, olfactory and inertial directional cues during displacement -”.

The newts were taken 1) 23 km from the E-ESE (103°); the orientation was 126° - 0.52 (n = 19), or 2) 42 km from the SSW (207°); the orientation was 221° - 0.59 (n = 18).

I.e. in the tanks the newts performed a navigatory act probably based in magnetic or celestial cues (olfaction seems too improbable) and the course was transferred to a magnetic compass which was the one in use when tested indoors.

As the declinations in the laboratory area is -0.16° compared with the home-area in the SSW-newts and +0.09° in the ESE-newts this can be taken as an indication of a bi-coordinate navigation system based on inclination and declination (however, P never mentions this possibility).

P. (1996) is a theoretical paper about magnetic navigation.

A most valuable paper which refers critically to the literature about navigation in newts, alligators, silveryeyes, turtles and pigeons.

P clearly believes in the possibility of (at least one-coordinate) magnetic navigation within a distance of 5-10 km from home – at least under certain circumstances with steeper local gradients than on the average. In this connection he mentions for the actual breeding ponds of the newts investigated that “*The local gradients of total intensity in the vicinity of these ponds also tends to be*

2-4 times steeper than the regional gradient, and therefore, could potentially provide greater accuracy in determining geographic position during local movements”.

On the other hand, P gives no values for ground level magnetic gradients for the ponds 42 km. towards SSW or 22 km. towards ESE, and therefore it is not possible to evaluate the surprising homeward orientation in particular in the ESE-newts (the orientation should be SSE-S for both populations in a mono-coordinate system).

Fischer et al. (2001) About simulated displacements $\pm 2^\circ$ in magnetic inclination for a SSW-population (45 km). The orientation is reversed for the newts “displaced” -2° , i.e. we have strong indications for a navigatory response where the magnetic inclination is one of the coordinates/gradients.

Also tested is the influence on the shoreward orientation, and nothing is found, i.e. the homing response seems independent of the shoreward response.

Lohmann & Lohmann (1996) is mentioned as demonstrating the use of two coordinates of a navigational map (i.e. total intensity and inclination) in baby turtles, but F et al. forget to tell that these two gradients are running (almost) in parallel in Indiana.

P et al. (2002) About “fixed-axis” magnetic orientation.

If newts in the tanks are temperature treated for displaying a **homing** response were exposed under long-light-waves (more than 500 nm) and then tested under full or long-waves the response in both cases is bimodal NNE-NE/SSW-SW; $38^\circ/218^\circ - 0.40$ ($n = 26$) and $26^\circ/206^\circ - 0.56$ ($n = 24$) under full and long-waves, respectively. However, the description (i.e. concentration) is better/higher when tested in reference to whether the newts came from home in ESE ($261^\circ/81^\circ - 0.53^{**}$, $n = 20$) or SSW ($17^\circ/197^\circ - 0.59^{***}$, $n = 30$), respectively (home-direction 360°). The better description in reference to 1) home-direction compared with 2) treatment (wave-length) is – also – clearly seen when the four sub-groups are related: a) ESE, full: $8^\circ/188^\circ - 0.46$ (11), b) ESE, >500 : $8^\circ/188^\circ - 0.63$ (9), c) SSW, full: $53^\circ/233^\circ - 0.59$ (15), d) SSW, >500 : $36^\circ/216^\circ - 0.63$ (15).

Doubling the angles leads to a significant difference between the two combined sub-samples according to 1), home directions ($P < 0.05$ both when applying the W-W-test or the M-W-W-test).

P et al. thus overlook that the fixed-axis is not the same for the two populations (home directions). Furthermore, the axial response “contains” the home direction in the SSW-population, whereas the axial response is about at right angles in the ESE-population. The right angle response may have something to do with the minute difference between the inclinations in the home and in the laboratory area.

Furthermore, P et al. do not comment upon the remarkably high sub-group concentrations after doubling the angles. The concentrations calculated correspond to $r = 0.80 - 0.90$ in a unimodal distribution before angle doubling. This is far higher than in any unimodal sample so far (and after) presented by P et al..

P. et al. (2002) Behavioral titration. Compared with the inclination in the testing/laboratory area further changes in inclination besides $\pm 2^\circ$ are investigated (-0.15° and -0.48°). The responses are dis-orientation and $25^\circ - 0.52^{***}$ ($n = 30$), respectively.

If mono-coordinate navigation rooted in magnetic inclination the responses should be \pm N/S or \pm NNW/SSE. However, this is not so as the axis is found to be NNE-NE/SSW-SW.

If bi-coordinate navigation where the second coordinate/gradient is the (magnetic) declination the declination response should be W in all four cases and this means SSW-SW for $+2^\circ$, W for -0.15° , NW(-NNW) for -0.48° , and NW-NNW for -2° . However, these orientations are not observed, and

the conclusion should be that **both propositions about magnetically based mono- or bi-coordinate systems are not fitted by the results.**

P et al. say that the inclination at the home pond is **measured** as -0.17° compared with the inclination at the tank/test site. As the home pond is 42 km in the direction of 207° as seen from the tank/test site it may be calculated that the differences in inclination at the E-ESE-pond compared with the tank/test site is -0.02° if the inclination gradient is running N/S and -0.09° if running NNW/SSE.

Obviously, the demands for using the magnetic inclination as one of the coordinates/gradients in a navigation system puts a lot of pressure on the skills of the newts. However, P&B (1994) mention that 0.1° deviation from horizontal when testing the newts results in “*strong orientation biases that masked any response to the magnetic field*”. Clearly, if proper orientation of the newts is influenced by so small differences in inclination their sense of vertical/horizontal should be close to absolute.

Discussion

In these years magnetic orientation and navigation are heavily announced in both scientific and public media.

Certainly, we should be engaged and positive about this phenomenon complex, but perhaps sometimes some of the good news are somewhat overrated or distorted. In particular, this seems to hold true in case of claims or indications of magnetic navigation in pigeons. Furthermore, whereas there seems to be no doubt about an influential magnetic compass in migratory birds, both the compass mechanism and the role and importance of the magnetic compass seem to be or could be different from the scenarios repeatedly envisioned by the leading scientist W. and R. Wiltschko.

It is extremely difficult to overview the concepts, systems and all the different animal species. Therefore people are relatively free to claim and argue for almost everything.

I find it very difficult to understand that a hatchling turtle (Lohmann) already from the very start and on basis of a conditioned response to the magnetic compass is able to produce an appropriate magnetically based navigational response intended for a situation in the remote future. The proposal of magnetically based gradient-navigation/homing in the newts of Phillips and co-workers looks convincing but their total of papers, procedures, reservations and different reactions and compasses appears very complicated and impenetrable for an average brain as the one of mine. It seems very important that Phillips and co-workers on the basis of measurements demonstrate the presence and potentiality of a magnetically based short-distance grid system around the home-ponds of the newts, i.e. follow the same way of strategy as Wallraff who demonstrated the presence of a potentially usable olfactory grid system in pigeons.

There seems to be no doubt that various animals including turtles, lobsters and newts use the magnetic field as a compass reference, and also that changes in magnetic inclination and intensity at least sometimes are influential on the subsequent orientation. However, the question is whether true coordinate/gradient-navigation is carried out or whether more simple motivationally induced compass reactions – standard, reverse or right angle (cross-axis) – are involved. Clearly, the same question could be asked in case of reports on olfactory or stellar navigation (e.g. Rabøl, J. 1998: Star navigation in Pied Flycatchers *Ficedula hypoleuca* and Redstarts *Phoenicurus phoenicurus*. – Dansk Ornith. Foren. Tidsskr. 92: 283-289).

On beforehand no one should expect magnetic navigation in Red-spotted Newts which seldom move away more than a few kilometers from the home pond. We should expect olfactory navigation

or perhaps acoustical “navigation” based on e.g. the frog-chorus from the home pond (if the newts are able to hear?). Perhaps also some kind of “navigation”/piloting based on the landscape texture, slopes etc. Probably the newts will also be able to use magnetic and solar (not stellar) based compasses. In fact, newts should be among the most remote candidates for making use of magnetic navigation, whereas albatrosses – because of their extremely wide foraging areas (with acceptable magnetic grids at least in some areas, see Åkesson & Alerstam 1998: Oceanic navigation: are there any feasible geomagnetic bi-coordinate combinations for albatrosses? – J. Avian Biol. 29: 618-625) - should be among the most obvious candidates. However, according to e.g. Mouritsen et al. (2003)* albatrosses do not seem to make use of magnetic navigation for finding their way back to the breeding island. A recent paper from Nevitt (2008)** suggests the same.

* Mouritsen, H., K.P. Huyvaert, B.J. Frost, and D.J. Anderson (2003): Waved albatrosses can navigate with strong magnets attached to their head. – J. Exp. Biol. 206: 4155-4166.

** Nevitt, G.A. (2008): Review. Sensory ecology on the high seas: the odor world of the procellariiform seabirds. – J. Exp. Biol. 211: 1706-1713.

The magnetic inclination is **measured** as 68.55° in the tank/test area, and as 0.17° lower in the home-area 42 km towards SSW. The normal change along the gradient is said to be $0.005^\circ/\text{km}$ (inclination) and $0.01\%/\text{km}$ (total intensity).

P gives no large-scale gradients for Indiana, US but following the map in Alerstam 2003: The lobster navigators. – Nature 421: 27-28 (comments to the Spiny Lobster paper of Boles & Lohmann 2003: - Nature 421: 60-63) these may be estimated to N/S or NNW/SSE for the inclination and NNW/SSE for total intensity.

One may wonder how it is possible to navigate from a distance of 20 km to the E-ESE of the tank/test area as the differences in both inclination and intensity must be extremely small.

In a **mono-coordinate** navigation system – based on magnetic inclination – the orientation of newts from both home-sites (SSW and E-ESE) should be about the same, i.e. S or SSE. However, in both cases the orientation is about home-directed. Therefore a **bi-coordinate** navigation system could be suspected, where the most obvious candidate for the second gradient/coordinate should be the **declination** (i.e. the angular difference between the direction towards magnetic N and geographical N). The declination may in principle be established within the tank where geographical N is established in reference to the sun (probably the newts cannot use the starry sky). However, the difference in declination following the displacement is very small (about 0.09° for the eastern and 0.16° for the southern population).

If we accept the probability for **short-distance magnetic navigation** in newts, lobsters and pigeons then **short-distance celestial navigation** in migrant birds should also be possible (because the gradient changes are of the same order of magnitude: latitude $0.01^\circ/\text{km}$ and longitude $0.015^\circ/\text{km}$ at latitude 40°N).

An open question is whether there is some sort of connection between shoreward and homeward orientation, i.e. whether the first in some way is a “responsible” for the latter which therefore is spurious in some way.

A possible solution could be to replace the rectangular tanks with a single shore in one of the long ends with a **radial-symmetrical tank** with land or water in the middle. Furthermore, we need cross-experiments of two kinds: 1) Displacements to the tank/test area also from home-ponds towards (about) N and W, and 2) displacements of newts from the same home-pond/population in four cardinal directions (as in pigeons as initiated by Wallraff). It must be possible to construct a transportable testing device which may be sufficiently horizontal (see below).

P mentions several times that it is necessary for the newts to scan the magnetic field in the home-area in order to establish the gradient-axis. However, this knowledge may in principle be inherited as e.g. a certain angle in reference to the magnetic compass.

Apart from the **fixed axis** orientation of P et al. (which in fact should be split in two different axes for the SSW- and the E-ESE-population), there seems to be nothing like a PCD as described by Wallraff in pigeons. At least, there is no (obvious) PCD/fixed axis for the newts of P et al. (2002) “displaced” 0.15° back towards the home pond from the tank/test site.

We desperately need **measurements** of the magnetic vector from multiple sites within the home area of the two newt populations.

Conclusion

For a first consideration the results of P et al. very clearly indicate to that the Red-spotted Newt makes use of magnetic coordinate/gradient navigation – and in particular that the inclination is an important variable (perhaps the newts are not measuring the inclination as such but measure the horizontal and vertical component of the magnetic vector; inclination = inverse cosine (horizontal/vertical intensity)).

However, as the newt under natural circumstances (the very small home-range) seems to be an utmost unlikely candidate for carrying out magnetic navigation we have to be cautious. **Perhaps the results of the investigations are not relating to natural circumstances but are spurious outcomes of the treatment and testing procedures selected and developed.** In particular it seems strange that the newts from the home-pond about 20 km in the direction of E-ESE as seen from the tank/testing area should be able to make use of the magnetic inclination as one of the gradients/coordinates because the difference in inclinations between the home-pond and the tank/testing site is extremely small. Furthermore, it seems unbelievable that the minute differences in declination (angular difference between the directions towards magnetic N and geographical N) could be used by the newts as basis for the second coordinate/gradient. In this connection I noticed the claim by P. that even a slope of 0.1° deviating from absolute horizontal in the arena when testing the newts will mask any magnetic influence. What should the poor newts then do under natural circumstances?

P. et al. have demonstrated/claimed two kinds of magnetic compasses (based in inclination and polarity, respectively), both shoreward and homeward orientation dependent of the wave-length of light, and both shoreward and homeward responses depending on season and temperature treatment while spending the time before testing in the water-tanks. Clearly, there is some connection between the two kind of compasses, and P et al. offer an explanation which may be true or not. We do not know by sure whether there is a connection between a cross-axis shoreward orientation and the homing response. My personal view is that there is no such connection, or at least that the homing orientation cannot be explained in a simple way as spurious shoreward orientation.

On the one side P et al. seems very honest and informative about the problems of magnetic navigation. On the other hand they also omit some paramount procedures (such as measurements of the magnetic vector in the home-pond area, and displacements from the four cardinal directions) and discussions (the problems with magnetic navigation from the E-ESE-home-pond). They developed into specialists in newt orientation and therefore always may have explanations for everything. In this connection I do not like their information that “*The animal Orientation Research Facility at Indiana University was designed specifically for studies of magnetic reception and*

magnetotactic orientation". Such an ambition put a lot of pressure on the scientist working there for reporting magnetic orientation, real or spurious.

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