The moving goal area and the orientation system of migrant birds

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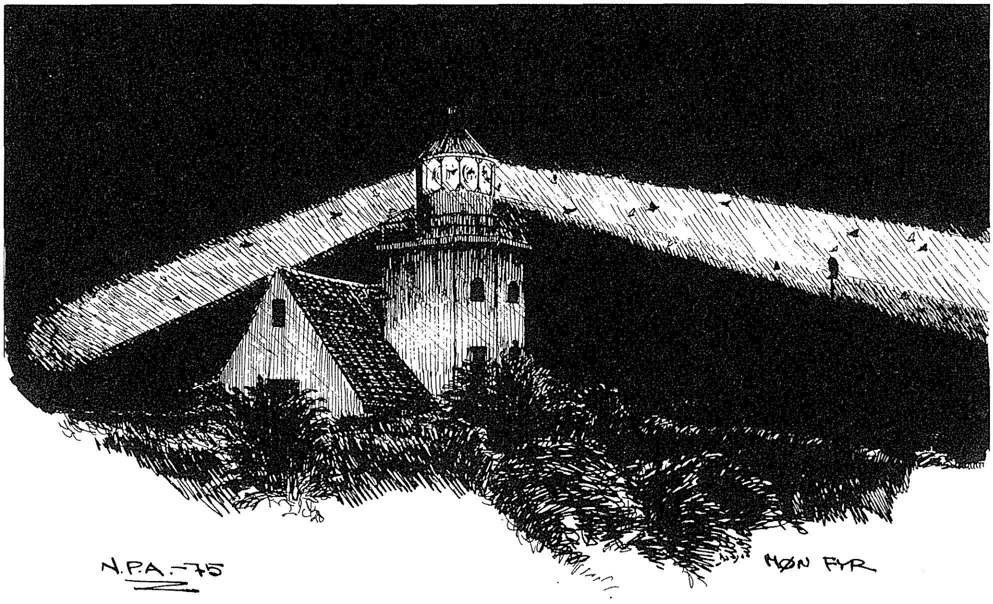
(Med et dansk resumé: Målområdet og trækfuglenes orienteringssystem)



Introduction

More than ten years ago I proposed the hypothesis of the moving goal area – especially with reference to longdistance Passerine migrants (Rabøl 1969, 1970).

The idea of the moving goal area became intimately coupled to 1) an orientation mechanism based on coordinate navigation inherited as a program, and 2) the presumed influence of stellar cues and a fixed internal clock, i.e. a clock temporarily inaccessible to the influence of extrinsic factors (e.g. Rabøl 1980).

However, the hypothesis of the moving goal area was born into a world of much sound scepticism against coordinate navigation based on inborn information – and especially such of stellar origin: In part, the claim of Sauer (1957) and Sauer & Sauer (1960) having demonstrated an inborn stellar coordinate navigation system was not well documented (Wallraff 1960a, 1960b, and see later). However, the experiments of Sauer simulating longitude-displacements on the stellar sky are difficult to interprete without involving the process of stellar based coordinate navigation (e.g. Emlen 1975).

Besides experimental results which were interpreted in terms of coordinate navigation, the point of my proposal concerning the moving goal area navigation hypothesis was based on the belief in *increased survival* in birds, i.e. genotypes endowed with such a program. Only relying on a one-direction orientation program seemed too hazardous for an inexperienced juvenile long-distance migrant with a complex or at least not straight-lined migratory route.

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Later on, the concept of one-direction orientation extended and developed into the clock-and-compass hypothesis (e.g. Gwinner & Wiltschko 1978). This is a model based on inherited information of the timing and duration of the migration and the migratory direction course as function of the season. The migratory direction is considered as the outcome of one-direction orientation. The clock-and-compass hypothesis has received general acceptance (e.g. Schmidt-Koenig 1979, Alerstam 1982).

Recently, Kiepenheuer (1984) has proposed the *magnetoclinic-course* hypothesis as another extension/modification of the one-direction orientation concept.

Of course, accepting the clock-and-compass model or the magnetoclinic-course hypothesis is not – necessarily – tantamount to rejecting a coordinate navigation program present in the same genotype!

The moving goal area as a center of maximum survival

It is important to realize that the moving goal area may be followed by means of processes originating in several orientation systems, e.g. a system based on coordinate navigation and/or a clock-and-compass system (Rabøl 1980 (Fig. 1)).

There is no urgent need for a coupling between a moving goal area and the process of coordinate navigation. The crucial point is that *irrespective of the orientation system there exists a moving goal area – understood as a center of maximum survival* (Figs 1-2): At a given time of the year birds *within* a certain area survive better than birds from the same population *outside* that area.

In the course of the year the goal area moves through the migratory route. Sometimes – as during the breeding and winter seasons – the area does not change position for some time.

Experimental evidence of the orientation system

It should be stressed that the experimental evidence of all orientation models mentioned above is weak or controversial.

1) The clock-and-compass hypothesis

The amount of migratory restlessness of caged warblers is positively correlated to the length of the migratory route (e.g. Berthold 1977). The duration of the migratory restlessness as well as the circannual clock seem to be modified – in a poorly understood way – by the light/dark regime experienced by the bird (Klein 1980).

It seems clear that the autumn and spring standard directions are roughly described in the genes with magnetic North as a compass reference – at least in the Garden Warbler *Sylvia borin* (Gwinner & Wiltschko 1978, 1980), and in the Pied Flycatcher *Ficedula hypoleuca*

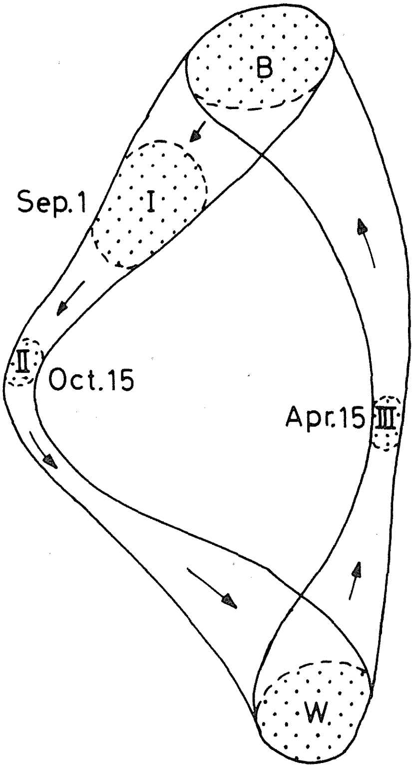

Fig. 1. The migratory progress of a population breeding in area B and wintering in area W. During the year the goal moves through the migratory route. 1 Sep. the goal is in I – and large. During certain parts of the year – e.g. 15 Oct. (II) and 15 Apr. (III) – the extent of the goal area may be much smaller. During summer and winter the goal area remains stationary in B and W. The small area, II, could be part of the Iberian peninsula if e.g. the European population of Pied Flycatchers *Ficedula hypoleuca* is considered. This area is an important fuelling station before the long trans-Saharan non-stop flight.
De prikkede områder viser udstrækningen og beliggenheden af en bestands målområde i yngletiden (B), 1. sep. (I), 15. okt. (II), og om vinteren (W). Der er tale om et konstrueret eksempel, og andre bestande har andre trækruter/målområder.

(Beck & Wiltschko 1982). In a similar way stellar North (the rotational axis) may possibly serve as an inborn compass reference for the standard direction in the Indigo Bunting *Passerina cyanea* (Emlen 1975), in the Pied Flycatcher (Rabøl & Dabelsteen 1983, Bingham 1984), and in the Garden Warbler (Wiltschko 1982).

However, there are serious problems with the predicted directional shift from »SW« to »SSE« in both the Garden Warbler and the Pied Flycatcher.

In these experiments nestlings from Germany were handreared and caged throughout the autumn. The orientation was registered in Frankfurt-cages or Emlen-funnels without sight of the stellar sky.

Gwinner & Wiltschko (1978) are claiming a directional shift from »SW« to »SSE« in the Garden Warbler – though admitting that the results are complex and open for different interpretations. Experiments from four autumns were pooled, and the total orientation in August/September was compared to the total orientation in October/December. As an average of the four years – and using a less crude seasonal division – the directional shift, however, is not from »SW« to »SSE« but from »S« to »WNW« (end of September) and then back to »SE« (Fig. 3). Furthermore, the variation between the autumns seems too large to permit pooling of the material. In the autumns with westerly orientation most experiments were carried out early in the season, whereas in the autumn of 1975 with much easterly orientation most experiments were late in the season. Only for that reason the pooling of all autumns produces a spurious counterclockwise directional shift in course of the season.

The migratory route of German Pied Flycatchers is »SW« to Spain/Portugal and then later on »SSE« to the African wintering ground. However, Beck & Wiltschko (1982) did not find such a shift in the orientation of captive flycatchers. On the contrary, the orientation in August was towards »SSE« and later on in September/October towards »S-SSW«.

In a recent investigation by Beck (1984), the predicted shift in orientation from SW to SE occurred in a group of Pied Flycatchers which in course of the autumn experienced decreasing magnetic intensities and inclinations corresponding to the values met under a normal migratory progress. The control group experiencing the unaltered German magnetic intensity and inclination throughout the autumn failed to develop SE-orientation in late autumn. Beck reports on dis-orientation in the control birds but another interpretation could be bimodal orientation around SSE and NNW. Further experiments are much needed in order to verify/repeat these experiments – and elucidate the coupling between the three variables: Season, magnetic intensity and magnetic inclination.

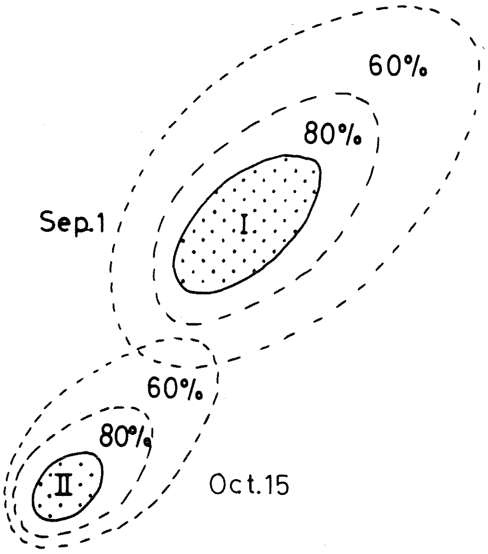

Fig. 2. A more detailed consideration of the goal areas I and II of Fig. 1. Within the fully drawn central area the survival is maximal, i.e. birds of the population which on 1 Sep. and 15 Oct. are within these areas experience the maximum survival – either immediately or in the long run. The chance of survival in the two rings outside the central area is 80% and 60% of the maximum.
I og II viser de samme målområder som i Fig. 1. De stiplede ringe symboliserer, at målområderne er diffust afgrænsede. Således betyder 80%-ringen omkring I, at fugle fra bestanden, der befinder sig her 1. sep., har mindre overlevelses-chance – nemlig 80% – end fugle fra bestanden, der på samme tidspunkt befinder sig indenfor den prikkede oval benævnt I.

Ironically, the single Lesser Whitethroat *Sylvia curruca* – which Sauer (1957) claimed to display stellar coordinate navigation – appears to provide the most clearcut example of a simple directional shift in course of the autumn following the shift (»SSE-SE« to »S«) in the migratory route (Gwinner & Wiltschko 1980). On basis of Wallraff (1960a) I have calculated the correlation coefficient between the nightly mean orientation and the date of the

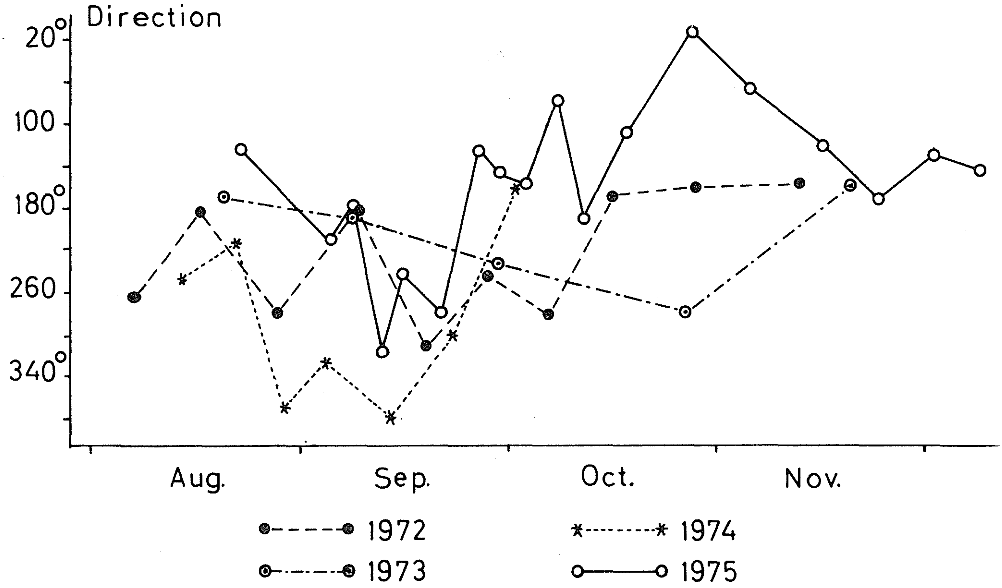

Fig. 3. The orientation of Garden Warblers *Sylvia borin* throughout four autumns. For each year the mean vector direction and the mean date of experiment were calculated for groups consisting of 10 birds. The groups were composed of the first 10 birds/experiments of the seasons, then the next 10, and so on. There seems to be a general tendency to a clockwise shift in the orientation until about 20 Sep., whereafter the orientation shifts counterclockwise towards SE. However, the material is heterogeneous from year to year in respect to both the orientation and the seasonal distribution of the experiments. This makes an overall pooling of the material dubious and a simple general conclusion very difficult. The data were kindly supplied by Gwinner and Wiltschko.
Gwinner og Wiltschkos orienteringsforsøg med unge Havesangere i de 4 efterår 1972-75. Hver prik (kryds) står for gennemsnitsretningen af 10 fugle. Orienteringen skifter fra S mod VNV og derfra »tilbage« igen mod SØ i efterårets løb. Ved at slå de 4 år sammen og se på orienteringen før og efter 1. oktober, når G og W frem til, at orienteringen skifter fra SV til SSØ – svarende til retningsskiftet i trækruten, da tyske Havesangere først trækker SV til Spanien og senere SSØ til tropisk Afrika. G og Ws analyse er imidlertid »ulovlig«, hvorfor man ikke kan fæstne lid til deres konklusion.

experiment. The orientation shifted significantly clockwise during the season (r = 0.84, n = 14). The significant correlation (r = -0.69) between the orientation and the latitude might be explained as a spurious one: After elimination of the date the partial correlation coefficient between orientation and latitude decreased to -0.12, which is quite insignificant.

2) The magnetoclinic-course hypothesis

Kiepenheuer (1984) considers this hypothesis as a simplification of the clock-and-compass model. The hypothesis is based on the inclination (dip) of the earth magnetic field, and the migratory directions are expressed in relation to the magnetic compass.

According to Kiepenheuer (p. 84): »The bird does not determine the north direction at all but simply flies on its innate migratory course by keeping *the apparent angle of dip at a constant value*«. This strategy produces a due S-course or steady curved tracks from E (ESE,SE) towards SSE (S), or from W (WSW, SW) towards SSW (S). Kiepenheuer mentions many migratory routes which develop according to his hypothesis, but forgets to tell about the great many other migratory routes which do not develop according to the expectation. To mention just a few conditions and examples: At the northern hemisphere routes cannot shift from e.g. 1) SW over S to SE; or start towards e.g. 2) north of E and later on bend southwards to directions south of E. According to the expectations of Kiepenheuer British Pied Flycatchers are misbehaving when starting towards SSE to Belgium/France then bending SW to Spain/Portugal and finally SSE-SE to Zaire. An example from the real world of 2) could be Spanish Redbacked Shrikes *Lanius collurio* starting ENE, then later on bending SSE and S towards the Eastafrican wintering ground.

Also the different autumn- and spring migratory routes – apparently the general rule among populations/species migrating between Europe and tropical Africa – speaks against the hypothesis of Kiepenheuer (which predicts strictly reverse routes autumn and spring).

It seems to me that topographical/ecological »stress« is much stronger than orientational »stress« (i.e. the demand of simplicity in the orientation system) in shaping the course – and timing – of migratory routes. Also the claimed simplicity of the magnetoclinic-course hypothesis compared to the clock-and-compass model is highly questionable. I wonder whether a migrant bird perceives the former system more simple?

According to the expectation of Kiepenheuer the orientation of the Garden Warblers of Gwinner and Wiltschko (Fig. 3) should *not* shift in course of the autumn but should continue on the initial SW-course (as the birds are retained in Germany). However, the orientation certainly shifts in course of the autumn – though not in the simple manner predicted and claimed by Gwinner and Wiltschko.

Also the experiments of the Wiltschkos (Wiltschko 1968, Wiltschko 1972, Wiltschko & Wiltschko 1972) fail to support the hypothesis of Kiepenheuer. In these experiments a control group of Robins *Erithacus rubecula* was compared to an experimental group in which magnetic inclination was lowered. In 10 such experimental series I calculated the correlation coefficient between the observed directional shift and the expected directional shift according to the hypothesis of Kiepenheuer. The correlation coefficient turned out to be quite insignificant – and even negative (-0.13)!

Before accepting the magnetoclinic-course hypothesis we have to wait for much stronger experimental support, but almost certainly the system is not so basic in the migratory process as Kiepenheuer seems to believe.

3) Coordinate navigation

There is increasing evidence of the existence of coordinate navigation, i.e. navigation based on comparison of stimuli perceived at the release or experimental site and some memorized home or goal values:

a) Homing pigeons make use of an olfactory gradient/coordinate in their homing process (Wallraff 1980b). Olfactory cues picked up en route during the transport *also* seem to play an important role – especially in Italy (e.g. Baldaccini et al. 1982, Papi 1982). However, this influence shows in the departure directions only, and not normally in the homing performance and speed.

Concerning migrant birds I do not believe in olfaction as a cue for coordinate navigation towards a goal area – except when this is a familiar site such as the breeding ground. Wallraff & Hund (1982) and Fiaschi et al. (1974) have demonstrated decreased homing ability in Starlings *Sturnus vulgaris* and Swifts *Apus apus* subjected to olfactory nerve section.

b) In the homing pigeon reverse vector navigation established in relation to inertial and magnetic cues perceived en route during the displacement seems to be of minor importance – or to have an effect only on the departure directions (Papi et al. 1978, Kiepenheuer 1978, Wiltschko et al. 1978, Papi et al. 1980, Wallraff 1980a, Wallraff et al. 1980, and Benvenuti et al. 1982). Wiltschko & Wiltschko (1982) render it probable that route reversal (i.e. reverse vector navigation) is used by very young and inexperienced pigeons, whereas coordinate navigation takes over in older birds. They do not mention the compass used in route reversal, but they certainly believe in the magnetic compass – and also seem to perceive the magnetic field as being at least part of the navigational map.

c) In my own displacement experiments using nightmigrating Passerines (e.g. Rabøl 1975), an appropriate compensation is positively correlated to the sight of the starry sky at the experimental site. When the sky was overcast, compensation was normally lacking, but reverse orientation often occurred. However, in these experiments compensation is not a proof – only an indication – of stellar based coordinate navigation.

d) The orientation of Redstarts *Phoenicurus phoenicurus* and Garden Warblers following a simulated displacement in a planetarium (Rabøl 1981b) is indicative of a system based on coordinate navigation towards a goal. As the experiments were made in the spring this goal, however, could be an imprinted position, e.g. the breeding area.

e) The directional shift in the Pied Flycatcher described by Beck (1984) might be perceived as the outcome of a navigatory process, either: a) a simple sort of mono-coordinate navigation (SW-orientation above a certain threshold of magnetic intensity and/or inclination, and SE-orientation below this threshold), or b) a simple sort of bicoordinate navigation in which the magnetic intensity and/or inclination is one coordinate signalling W- or E-orientation (above/below a certain threshold-value), and the season is the other »coordinate« signalling S in autumn and N in spring.

Of course, several experiments may be interpreted as a total lack of coordinate navigation. But negative evidence is mostly no evidence in the case of a complex and redundant system.

Among the surprising (?) results are the classical displacements of Crows *Corvus corone* (Rüppell 1944). The distribution of recoveries is indicative of a system based on one-direction orientation – which is unexpected as the birds were trapped on their way back to the breeding area.

Also the S-SSW-orientation of the *adult* Robins following a displacement to the Canary Islands should be recalled (Rabøl 1981a). At least once these birds had wintered in the western Mediterranean NE of the Canaries.

These Crow- and Robin-results are surprising as almost all authors believe in a sort of imprinting on the coordinate values of the breeding area and wintering ground (e.g. Perdeck 1958, Rabøl 1981a).

In conclusion, the existence of coordinate navigation in the orientation system of, at least, homing pigeons is considered highly probable. The question is whether the compensatory orientation in displacement experiments with migrant birds is the result of reverse vector navigation (or more simple: contains a component of reverse one-direction orientation) or coordinate navigation. As discussed

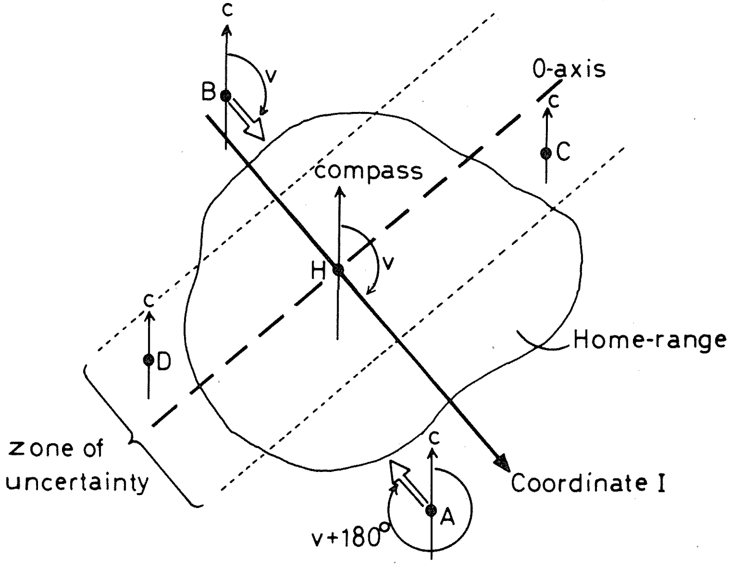

Fig. 4. The principle in mono-coordinate navigation. H denotes the home/goal and the fully drawn line encloses the home-range. The direction of a gradient (coordinate I) is established as the angle v in relation to a compass. A zero-axis and a zone of uncertainty are running at right angles to the coordinate. The orientation outside the zone of uncertainty is either v (B) or v + 180° (A).

En fugl bor i H og har et hjem-område (home-range), som den kender af erfaring gennem sin færden i området. Igennem H går en koordinat, der er fastlagt med vinklen v i forhold til et kompas, der f.eks. kan være magnetisk nord eller stjerne-nord. Koordinaten afspejler (f.eks.) retningen mod en stigende lydstyrke. Vinkelret på koordinataksen og gennem H er en 0-akse, hvor lydstyrken overalt er den samme, og omgivende 0-aksen er en usikkerhedszone (zone of uncertainty). Først når fuglen er udenfor usikkerhedszonen kan den afgøre, om lydstyrken er stærkere eller svagere end i hjemmet (den kan huske lydstyrken i H). Forflyttes fuglen til A eller B uden for hjem-området, slår den ind på en kurs som vist med de hvide pile. I A, hvor lydstyrken er stærkere end i H, flyver den i vinkel (v + 180°) – d.v.s. i koordinatens retning og væk fra lydkilden. I B, hvor lydstyrken bedømmes til at være klart svagere end i hjemmet, flyver fuglen bort i kursen v. Bemærk hvordan de to kurser bringer fuglen hjemad – ikke nødvendigvis direkte mod H, men i reglen vil den ramme hjemområdet, og så snart den er indenfor kendte omgivelser, er det en smal sag at finde hjem. Hvis den ikke – som ved start i C og D – rammer direkte ind i hjemområdet, kan den prøve sig frem den ene og/eller anden vej langs 0-aksen og indenfor usikkerhedszonen. Før eller senere vil den så ramme hjem-området.

by e.g. Rabøl (1978, 1980, 1981a) it is extremely difficult to solve the underlying orientation system in the compensatory reaction following a geographical displacement.

After being cautious and sceptical for some years I am now again almost convinced that coordinate navigation plays an important role in the compensatory orientation of displaced birds – but certainly my view of the process of coordinate navigation has altered through the years.

The no-man's-land between the concepts

The important point to stress is that the clear-cut distinction between one-direction-orientation and coordinate navigation shold be »softened«. Otherwise, it is difficult to avoid an attitude towards the two concepts being alternatives.

Instead the two concepts should be considered as the extremes of a continuum.

The fruitful way of thinking lies between the two ways of modelling. The one-direction concept has to be extended, whereas the concept of coordinate navigation has to be »devaluated«.

A major step in this development was the realizing of Wallraff (e.g. 1974) that coordinate navigation in birds is a process encumbered with uncertainty. Wallraff introduced such terms as zero-axis, zone of uncertainty and PCD (preferred compass direction).

Fig. 4 shows the course of a gradient constituting an axis of coordinate (I) established in relation to a compass-reference. When displaced to A from the home/goal (H) the bird perceives an increased 'intensity' of the stimulus constituting the gradient. The orientation in A is now simply v + 180° established in relation to the compass-reference. When displaced to B the bird orients in the direction of v – because it perceives a decreased »intensity« of the home-value of the gradient.

A and B are both outside the home-range and the zone of uncertainty. Within the latter – e.g. at the sites C and D – the bird is not able to detect whether the »intensity« has decreased or increased.

It should be noted that outside the zone of uncertainty the orientation is seldom exactly home-directed, but often leads towards the home-range. When reaching the zone of uncertainty outside the home-range the bird has to search one way or another along the zero-axis and within the zone of uncertainty.

Fig. 5 (upper figure) shows two coordinate axes (I and II) with zero-axes and zones of uncertainty. Within the latter the orientation is supposed to be *polarized* in one of the directions along the gradient/coordinate.

Fig. 5 (lower figure) shows the orientation in the 9 zones within and without the two zones

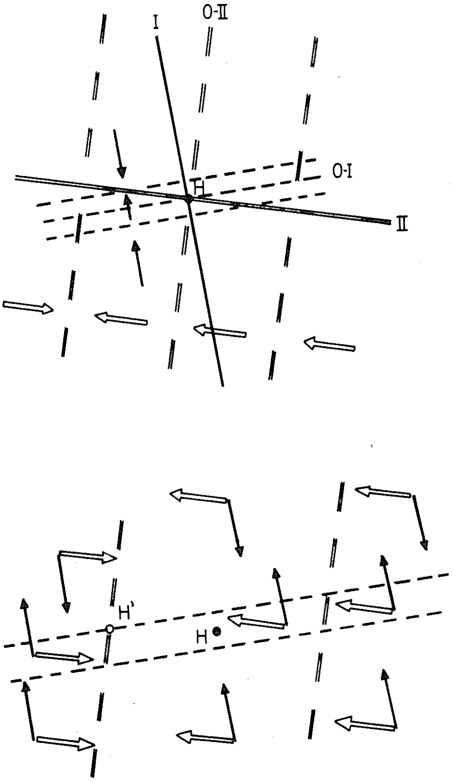

Fig. 5. The principle in bicoordinate navigation following the model of Wallraff. The upper figure shows the two coordinates I and II, the two zero-axes, and the two zones of uncertainty. The orientation within each zone of uncertainty is polarized in one of the directions along the coordinate. The lower figure shows the orientation within the 9 zones formed by the two zones of uncertainty. The overall orientation is converging towards H' and not towards the home/goal (H).

Wallraffs model af koordinat-navigation. Øverst ses hjemmet/målet i H og de to koordinat-akser I og II. Desuden de to 0-akser 0-I og 0-II med tilhørende usikkerhedsområder (afgrænset af de stiplede linier). Indenfor et usikkerhedsområde antages orienteringen at være ensrettet i den ene af de to retninger parallelt med koordinat-aksen. Nederst ses orienteringen i de ni zoner i og udenfor usikkerhedsområderne. De kombinerede retningsvalg ses at konvergere/pege mod punktet H' og ikke mod H.

of uncertainty. The combined resulting orientations (NE, SE, SW, and NW) are seen to converge towards H' – not towards the home/goal (H).

Before the modelling of Wallraff the process of coordinate navigation was mostly considered as an exact calculation of the direction from the experimental site towards the home. Such a view was an obvious obstacle in accepting birds – and especially juvenile, inexperienced birds – to be able to navigate towards a goal where they have never been before.

Now it is clear that the zone of uncertainty may be very wide, and the determination of a gradient/coordinate axis very rough. Also there may be not two but only a single coordinate in order for the system to work.

Figs 6-7 visualize the links between one-direction orientation and coordinate navigation.

Fig. 6A shows a standard direction (210°) established as one-direction orientation in relation to a compass-reference. Such a standard direction may be programmed to shift – e.g. to 140° – in the course of the autumn. This figure represents the traditional view of the orientation component in the clock-and-compass model.

However, in the real world *reverse* orientation and orientation at *right angles* are common phenomena, which should be considered as derivations of a mechanism where orientation in the standard direction is the dominant and most probable outcome (Rabøl 1978, 1981a, 1983).

Fig. 6B shows a vectorial cross consisting of standard and reverse orientation and orientation at right angles. The lengths of the four

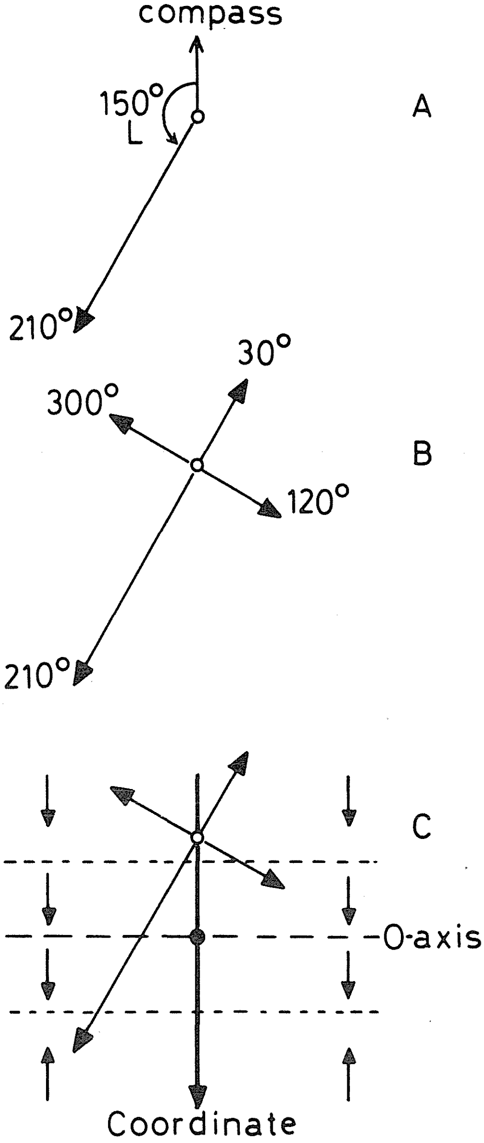

Fig. 6. The development from one-direction orientation towards monocoordinate navigation. A denotes a standard direction (210°) established as the angle 150° to the left of a compass. B denotes the cross-axis model: the orientation system is considered as vectorial probabilities of orientation in the standard direction (210°), the reverse direction (30°) and in the two directions at right angles (120° and 300°). C shows a combination of B and monocoordinate navigation in which the zero-axis is a line of equilibrium moving downwards during the season.
Øverst (A) ses retnings-orientering mod 210°. Denne kurs opretholdes ved at indtage vinklen 150° til venstre for en retningsgiver (compass), der kan være f.eks. magnetisk nord eller stjerne-nord. B viser den udbygning af det simple retnings-orienterings-system, der kan kaldes korsorientering. Pilenes (vektorernes) længde symboliserer/viser sandsynligheden for orientering i den pågældende retning: 210° (normaltrækretningen), 30° (omvendt orientering), og 120°/300° (vinkelret orientering). C viser en kombination af B et mono-koordinat-system (mono = én (akse)). I løbet af efteråret forskyder 0-aksen (ligevægtslinien) sig mod syd. Til sidst stopper den som signal på, at trækfuglen skal stoppe (vinterkvarteret er nået). Koordinaten kan tænkes baseret på information fra sol- eller stjernehimlen, eller Jordens magnetfelt. Der er nok af muligheder, men om de udnyttes vides ikke – indtil videre.

vectors are functions of the season, the internal state of the bird and environmental influences.

Reverse orientation is liable to arise in stress situations (e.g. food lacking or handling in captivity), or following an overshoot (e.g. after a preceding migration in a tailwind). Orientation at right angles is often seen in a low motivational state (e.g. in the start or end of the migratory season), or when the polarity of the compass-reference is obscure, or in relation to a sideway drift by the wind (Rabøl 1983).

Fig. 6B illustrates the *cross axis model.* 210° could be the initial standard direction. As the season proceeds one or the other of the right angle components may become influential vectors. If the Garden Warbler (Fig. 3) is taken as an example the »NW«-component gradually takes over until late in September, and later on the »SE«-component manifests itself.

Fig. 6C shows a combination of the cross-axis and a mono-coordinate system. The zero-axis is moving south in the course of the season. The zone of uncertainty is wide – say several hundred kilometers. The gradient/coordinate may be formed by e.g. the altitude of the sun at midday, the altitude of the rotational axis of the stellar sky, or the earth magnetic intensity or inclination.

Fig. 7 rests on the model of Wallraff. The orientations within the zones of uncertainty are polarized towards S and W. The orientations in the four quadrants are converging towards H' (compare Fig. 5).

Fig. 8 shows the orientation in relation to geographic north and the home-direction (H) from 12 symmetrical sites in 3 circles around H. Close to the home (upper figure) the PCD is very pronounced and directed in the standard direction (SW). However, homeward orientation is totally lacking. Moving out from the middle to the outer ring the PCD diminishes in strength, and homeward orientation becomes more and more pronounced.

The polarized orientation within the zones of uncertainty may shift during the season and from autumn to spring: The standard direction follows the orientation of the PCD.

The difference between the models in Fig. 6B and 7 is that the initiation of reverse orientation and orientation at right angles in the cross-axis system is resting on an estimation or a *guess* of which way to orient. In the systems including coordinate navigation, the decision process is based on *measurements.* The errors are additive in the first system, whereas the zones of uncertainty provide a frame around the possible errors: there is true negative feedback in the systems which include coordinate navigation.

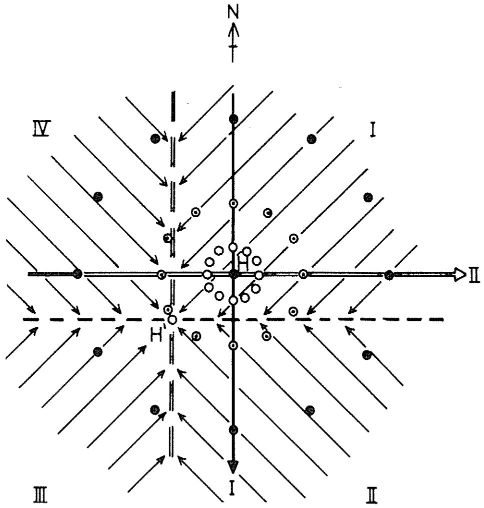

Fig. 7. A further development of Fig. 6: A bicoordinate navigation system in which the goal, H, is moving towards SW in the course of the season. The orientations within the four quadrants are converging towards H'. Normally the bird is located within quadrant I and orients towards SW – irrespective of the direction towards the goal, H. The orientation in relation to geographical north and the goal, H, in the 12 dots in the 3 rings around H is shown in Fig. 8.

Denne figur er en videreudvikling af Fig. 6. Man ser et mål, H, der med tilhørende koordinatsystem i løbet af efteråret bevæger sig mod SV. Orienteringen indenfor de 4 kvadranter (I, II, III og IV) konvergerer mod H'. Normalt befinder trækfuglene sig i kvadrant I, og er SV-orienterede – ganske uanset deres aktuelle position i forhold til H. Hvis en fugl overskyder H i betragtelig grad ryger den måske helt ned i kvadrant III og viser omvendt (NØ) orientering. Vinddrifter den mod højre eller venstre kan den ende i kvadranterne IV eller II og vise vinkelret (SØ/NV) orientering. De tre punkt-ringe er forklaret i forbindelse med Fig. 8.

The final remark should be that speculations (e.g. Rabøl 1978, 1980, 1981a, 1981b) whether one and/or another of the extremes is existing in a pure form should be avoided. In this way the question of how the migratory route is programmed cannot be answered. Instead, we have to realize that sometimes one and sometimes another model of description is appropriate for the understanding (Figs 6-7). The real world is not so clearcut or black and white as

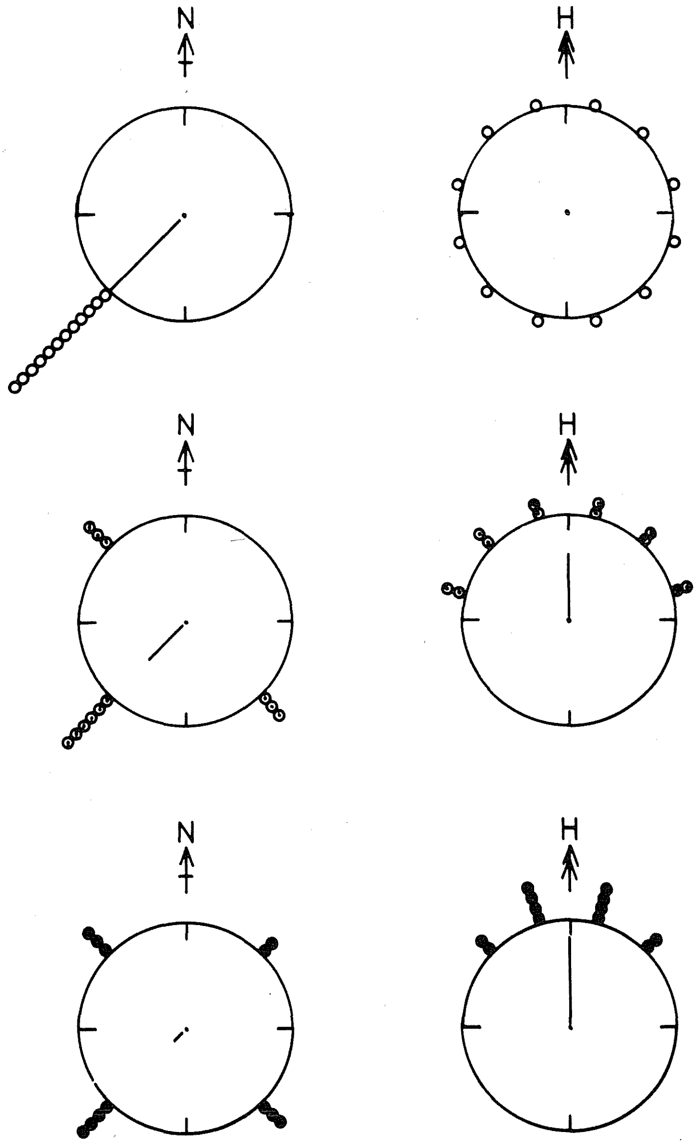

Fig. 8. The orientation at the 12 sites in the 3 rings of Fig. 7. Close to H (upper figures) the orientation is stereotyped towards SW – in the standard direction – whereas there is no homeward component. At some distance from H (the figures in the middle) the standard direction is still pronounced, and a clear homeward tendency is appearing. At long distances from H the orientation in the standard direction is almost disappearing, whereas the homeward orientation is very pronounced. The conclusion should be that normally the bird orients in the standard direction – and especially so if the zones of uncertainty are wide. If the progress/speed of the migrant bird and the moving goal, H, is about the same, and if sideway drift is corrected for, the displayed orientation is almost or totally indistinguishable from that resulting from one-direction orientation in the standard direction. However, if overshooting or sideway drift is exceeding certain limits, compensatory reverse orientation or orientation at right angles is carried out.
Retningsvalgene/orienteringen i de 12 punkter i de 3 ringe vist på Fig. 7. Tæt ved H (hvide punkter) er orienteringen stereotypt ensrettet mod SV (øverst til venstre), medens der ikke er nogen orientering i forhold til hjemretningen mod H (øverst til højre). I nogen afstand fra H (punkter med prik i midten) er den SV-lige normal-orientering stadig iøjnefaldende (i midten til venstre), og nu optræder der også en tydelig hjemrettet orientering (i midten til højre). I lang afstand fra H (sorte punkter) forsvinder normal-orienteringen næsten, medens hjem-orienteringen bliver særdeles udtalt.

the two extremes, one-direction orientation and coordinate navigation. One has to include reverse orientation, orientation at right angles and the PCD into the models. Just like in other fields of science we have to realize that apparently exclusive and incompatible models may describe important aspects of the same phenomenon.

Outlook

In order to test different models – or, rather, details of the complex orientational system – several experiments may be proposed:

1) The Garden Warbler experiments of Gwinner & Wiltschko (1978) have to be repeated – in order to test the clock-and-compass model. As almost all European Pied Flycatchers seem to move through Spain/Portugal before migrating S and SE to West- and Central Africa, this species seems promising. Also migrants – such as Lesser Whitethroat and Redbacked Shrike – migrating SE through Europe and later on bending S have to be investigated.

2) The magnetoclinic-course hypothesis (Kiepenheuer 1984) should be tested using migrants as their own controls: In an appropriate manner the magnetic inclination should be shifted from night to night.

3) In order to demonstrate the possible existence of stellar coordinates the planetarium-experiments of Rabøl (1981b) should be extended. An obvious procedure would be to habituate juveniles under a rotating planetarium sky mimicking the outdoor starry sky (autumn). After some nights the rotational axis of the planetarium sky should be decreased by e.g. 5°, simulating a displacement towards S. If the orientation then shifts from e.g. SSW to NNW this would be a strong indication of a stellar-based N/S-coordinate. Also clockwise and counterclockwise rotations of the planetarium sky should be carried out, simulating E- and W-displacements.

4) Following the same principle as mentioned in 3) different magnetic components – most obviously the inclination and the field intensity – should be decreased by e. g. 5° and 10% (autumn), simulating displacements towards S. If the orientation shifts from e.g. SSW to NNW this would be a strong indication of a magnetical based N/S-coordinate.

Chaffinches and Bramblings on the move. Photo: Erik Thomsen, Biofoto.
Trækkende Bog- og Kvækerfinker. Hvordan finder de og andre trækfugle vej? Det har man søgt at forklare ved forskellige modeller, men det eksperimentelle grundlag er svagt, og vi er længere fra en forklaring, end det almindeligvis hævdes.

5) Long-distance displacements of long-distance migrants should be carried out. I should like to displace juveniles of the following species, trapped on autumn migration in Denmark, to Kenya: a) Pied Flycatcher (wintering in West Africa and Zaire), b) Lesser Whitethroat (wintering in Sudan) and c) Thrush Nightingale *Luscinia luscinia* or Spotted Flycatcher *Muscicapa striata* (wintering mostly S of Kenya). The initial orientation should be N or NW in all the species but in the end of the autumn the orientation should be different: W (a), N (b) and S (c) – and *if so,* this would be a strong indication of coordinate navigation towards the wintering area.

Summary

Irrespective of orientation system there exists a center of maximum survival – the goal area – which in the course of the year moves through the migratory route.

Traditionally, the orientation system is viewed as either one-direction orientation or coordinate navigation. Such a dichotomy is considered inappropriate. The experimental evidence of both models is weak or controversial and several »hybrid«-systems may be proposed. Such systems could be cross-axis orientation and/or the »mild« form of coordinate navigation in the sense of Wallraff.

Resumé

Målområdet og trækfuglenes orienterings-system

Formålet med denne artikel er at belyse, hvad der kan kaldes en trækfugls overordnede mål her i tilværelsen. Desuden – og i forbindelse hermed – at nedbryde de kunstige skranker mellem to begreber: Retnings-orientering og koordinat-navigation.

Som en indgang til det første af disse punkter kan man betragte følgende situation: Hver sommer får et par Havesangere 5-6 unger, og i løbet af det følgende år afgår 5-6 af disse 7-8 fugle ved døden, således at vi i starten af næste yngleæson igen er tilbage ved de 2 fugle, yngleparret.

Der er flere årsager til denne meget store dødelighed, herunder et galt afstemt trækforløb: Fugle, der trækker gennem bestemte områder til bestemte tider af året, har større overlevelses-chance end fugle fra samme bestand, der passerer gennem andre områder og/eller trækker tidligere eller senere på året. Efter denne opfattelse er det overordnede mål/job for en trækfugl at være/befinde sig indenfor et bestemt område til en bestemt tid af året. Man kan sige, at en trækfugle-bestand har et *målområde,* der bevæger sig afsted i trækruten i årets løb (Fig. 1-2).

Man må her antage, at der i bestanden findes et udvalg af genetisk programmerede anvisninger/skitser, der resulterer i forskellige trækrute-forløb. Den naturlige udvælgelse sørger så hele tiden for at »luge« de galt afstemte trækforløb fra, og de (længst) overlevende trækfugle er så hele tiden dem, der er velprogrammerede og egnede til at klare deres job.

Efter denne opfattelse er yngleområdet – eller vinterkvarteret – ikke (nødvendigvis) overordnet andre målområder på trækruten: Trækfuglen skal jo hele tiden videre i sin årscyklus, og for at komme videre, skal den kunne overleve og klare sig godt, hvor den befinder sig her og nu. Det er selvfølgelig meget vigtigt at kunne finde et passende yngleområde – for her opformerer bestanden sig som »modvægt« mod den store dødelighed. Men det er sådan set lige så vigtigt for en bestand af langdistance-trækkere at kunne finde frem til et godt fourageringsområde, hvor de kan fylde brændstof (fedt) på tanken inden et flere tusind kilometer langt non-stop-træk over et stort hav- eller ørkenområde.

Spørgsmålet er nu ved hjælp af hvilket orienterings-system, trækfuglen finder sit målområde?

Målområdet behøver nemlig ikke være et mål i samme forstand som f.eks. Kastrup Lufthavn er det for et fly, der starter en non-stop flyvning fra New York. Målet behøver ikke være et geografisk/topografisk genkendeligt område, eller givet ved et sæt koordinat-værdier som f.eks. en bestemt breddegrad og en bestemt længdegrad. Et mål kan også være givet ved en vektor – eller en serie af vektorer: »Træk 2400 km mod SV«, eller »Træk først 1000 km mod SV, så 500 km mod SØ, og til sidst 1118 km mod NNØ (18,43°)«. Den sidste ordre vil medføre en tilbagevenden til udgangspunktet (hvis det foregår i et plan), og kan i princippet bruges til at følge et vandrende målområde som vist på Fig. 1. Naturligvis ved fuglen ikke, hvad 2400 km er for noget, men denne besked kan omsættes til f.eks. 60 timers træk med en hastighed af 40 km/time. En sådan besked kan tænkes programmeret i generne, ligesom retningen SV kan programmeres som »skråt væk til venstre for magnetisk nord«.

De fleste trækfugle-forskere forestiller sig, at de unge, uerfarne fugle benytter sig af et sådant *vektor-orienterings-*system til at følge det vandrende målområde – medens de gamle, erfarne fugle antages at navigere mod målområdet, i hvert fald når dette befinder sig i visse positioner som f.eks. yngleområdet, vinterkvarteret og vigtige optankningssteder.

Hvad trækfuglene har genetisk programmeret er altså ifølge denne opfattelse alene en retningssans og en evne til at koble afstande på retninger. Navigation er noget fuglene lærer undervejs i det praktiske liv.

Kardinal-beviset på vektor-orienterings-systemet er imidlertid svagt – i bedste fald marginalt og i værste fald helt manglende (Fig. 3). Den mest positive evidens for vektor-orienterings-modellen må siges at være, at man ved – eller formoder at vide – at trækfugle er i stand til i grove træk at holde en kurs i normaltrækretningen både forår og efterår i forhold til såvel magnetisk nord som stjerne-nord, samt at disse evner er medfødte, d.v.s. genetisk programmerede.

Problemet med vektor-orienterings-modellen er den usikkerhed, der ligger i at bedømme afstande, og hvor og hvornår kursændringer skal finde sted: Fejl hober sig op og bliver store, og efterhånden kommer fuglene (måske) i for stor uoverensstemmelse med målområdet, og dødeligheden stiger voldsomt.

Kiepenheuer har forsøgt at komme uden om kursændrings-problemet i den såkaldte magneto-cliniske hypotese: Fuglene fra en given bestand holder en bestemt (konstant) skrå vinkel i forhold til den magnetiske hældning (inklination). Det medfører så automatisk krumme trækruter. På afgørende punkter synes Kiepenheuers forsimpling af vektor-orienterings-modellen dog ude af takt med virkeligheden.

I stedet for at forsimple vektor-orienterings-modellen forsøger jeg så at udbygge den – så den kommer i bedre overensstemmelse med de faktisk observerede observationer.

Det første skridt i en sådan udvikling er at inkludere omvendt og vinkelret orientering i en retnings-orienteringsmodel. På Fig. 6 ses den såkaldte *kors-orienterings*-model.

Hertil kan så tilføjes en komponent af koordinat-navigation – i en simpel udgave som vist på og omtalt i forbindelse med Fig. 4, 5, 6, 7 og 8. Herved samordnes erfaringer/opfattelser fra brevdue-fronten (Wallraff) med trækfuglenes orienteringssystem.

Traditionelt har man opfattet retnings(vektor)-orientering og koordinatnavigation som to alternativer: Hvis den ene var rigtig, var den anden forkert – og omvendt! En sådan sort-hvid opfattelse er imidlertid ufrugtbar. For mange år siden førte fysikerne nogle hidsige debatter om lys skulle opfattes som en bølge- eller en partikel-bevægelse. »Sandheden« – d.v.s. det praktiske udfald – viste sig at være, at lys *både* kunne opfattes og beskrives som en bølge-bevægelse *og* som en partikel-bevægelse.

Selv om det kan forekomme vattet og ubeslutsomt tror jeg, at man må opfatte – og beskrive – trækfuglenes orienterings-system på en lignende både-og vis – i den forstand, at snart retnings(vektor, kors)-orientering og snart koordinat-navigation er den mest iøjnefaldende model for, hvad man måtte iagttage.

Til sidst skitseres nogle forsøg, der kan kaste lys over »detaljer« i et sådant komplekst orienterings-system. Mest påkrævet er forsøg designet til at vise indflydelse af navigatoriske koordinater (Fig. 6C). Også vektor-orienterings-modellen trænger til at bekræftes gennem nye forsøg.

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