———— **Commentary** ————

The role of visual landmarks in the avian familiar area map

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Summary

The question of whether homing pigeons use visual landmarks for orientation from distant, familiar sites is an unresolved issue in the field of avian navigation. Where evidence has been found, the question still remains as to whether the landmarks are used independent of the map and compass mechanism for orientation that is so important to birds. Recent research has challenged the extent to which experiments that do not directly manipulate the visual sense can be used as evidence for compass-independent orientation. However, it is proposed that extending a new technique for research on vision in homing to include manipulation of the compasses used by birds might be able to resolve this issue. The effect of the structure of the visual sense of the homing pigeon on its use of visual landmarks is also considered.

Key words: vision, landmark, homing pigeon, spatial memory, navigation.

Introduction

The mechanisms by which birds navigate for homing and migration was one of the most enduring research fields of the 20th century and continues to be so into the 21st century. The homing pigeon has been an ideal model for all aspects of avian navigation due to its ease of domestication and high motivation to home. Furthermore, pigeons display an ability to navigate from distant unfamiliar sites, which has made them the subject of a large part of the research on navigation mechanisms. Although many advances have been made, several aspects of the field remain controversial, and none more so than the role played by visual landmarks. It has often been hypothesised (Griffin, 1952; Matthews, 1963; Wallraff, 1974) that, as well as being able to navigate successfully from unfamiliar places, birds have a second homing mechanism known as a 'familiar area map' (Baker, 1982). This allows them to navigate successfully from places that they have previously visited on the basis of a memory of familiar landmarks. Birds might form a familiar area map because it provides some advantage, such as increased accuracy, over other navigation mechanisms. Alternatively, it might add to the redundancy of the navigation system, allowing them a further mechanism for homing when others are unavailable. The adaptive benefits are clear in either case.

Although there is no resistance on theoretical grounds to birds having a familiar area map, experimental evidence for the role of visual landmarks has remained equivocal. Some have concluded that visual landmarks are not required for homing (Schmidt-Koenig, 1979; Wiltschko, 1991, 1996; Wiltschko and Wiltschko, 1998; Walker et al., 2002). However, others have maintained that a role for visual landmarks in the familiar area map is a reasonable assumption (Bingman et al., 1998; Wallraff et al., 1999). Indeed, Wallraff et al. (1999) have stated that current evidence from one aspect of research is strongly in support of this view.

Despite the conflicting results obtained in experiments investigating the familiar area map, and the lack of a resolution, very few reviews on avian navigation pay more than lip service to the problem; normally, an argument for or against the use of visual landmarks is stated, without much attempt to review conflicting literature (e.g. Wiltschko and Wiltschko, 1998; Bingman and Able, 2002; Walker et al., 2002). Wallraff et al. (1999) is one of the few papers to directly address the conflict over this issue. However, new experiments have been published that require a re-examination of the evidence for and against the use of visual landmarks. It is the aim of this review to interpret what can be said about the role of visual landmarks in the avian familiar area map on the basis of current data. It will also propose how the extension of one of the techniques for research on visual cues might be able to resolve the issue.

Mechanisms of landmark navigation

It is well established that birds use the map and compass mechanism for navigation from unfamiliar places (Kramer, 1953). This involves locating the current position with respect to home (the map step) and then orienting in the direction required to reach home (the compass step). This has been

extensively reviewed elsewhere (Wallraff, 2001; Wiltschko and Wiltschko, 2003) but the main findings key to the present paper are that birds can use both the sun's azimuth and the earth's magnetic field as compasses, and atmospheric odours can provide navigational map information. Interestingly, birds made anosmic cannot orient from unfamiliar sites but are able to do so from familiar places (Benvenuti et al., 1973; Hartwick et al., 1977). This has been used as an argument in favour of a familiar area map (but see Benvenuti and Fiaschi, 1983).

The question with regard to orientation by visual landmarks is whether the familiar area map is an extension of the map and compass mechanism or not. If so, then compass bearings from landmarks would be used instead of compass bearings from the navigational map factors. A landmark map in which compass bearings from landmarks are used has been defined as a mosaic map (Wallraff, 1974; Able, 2000). The alternative to a mosaic map is that the visual landmarks are independent from the map and compass system and define the route to the goal themselves. This might be by the position of the goal relative to an array of landmarks (e.g. fly between the church and the hill to get home) or it might involve a learned route home *via* a 'chain' of landmarks (fly from the forest to the hill, then to the lake, etc., to get home). This type of orientation has most often been defined as piloting (Griffin, 1952), but some confusion has arisen as to exactly what mechanism is used in piloting (Able, 2000). The key point though is that this type of orientation does not require a compass (Papi, 1992). Being independent of the map and compass system, piloting would be valuable if the compass was providing inaccurate information or was unavailable. On the other hand, a mosaic map might require a smaller memory load, as it would require only a few compass bearings to be memorised rather than a large array of landmarks. Thus, there is no *a priori* reason to suppose that one or other of these mechanisms would be preferred.

One aspect of bird navigation provides a test that can distinguish between the two mechanisms. Birds use the sun's azimuth as a compass, and this is time compensated. Thus, if birds are released from unfamiliar places having had their day–night cycle artificially altered (i.e. clock shifted) then they vanish from a release site in the wrong direction (Schmidt-Koenig, 1960). The degree to which they deflect is dependent upon the length of clock shift. A 6-h shift leads to an approximate 90° deflection in the mean vanishing bearing from an unfamiliar release site, although the precise amount depends upon the time of day and year and is usually considerably greater than 90° in the summer months (Neuss and Wallraff, 1988). Fig. 1 demonstrates the vanishing diagram of a group of clock-shifted birds (taken from Holland, 1998). However, if birds are familiar with a release site from previous releases, and visual landmarks are independent of the sun compass, then full deflection might not be expected. Wallraff (1991) has proposed that if the birds recognised that the sun and landmarks were in conflict, then reduced or absent deflection might be expected, depending on whether the birds compromised between sun and landmarks or ignored the sun

Control: n=20
r=0.75
ϕ=251°

Clock shift: n=25
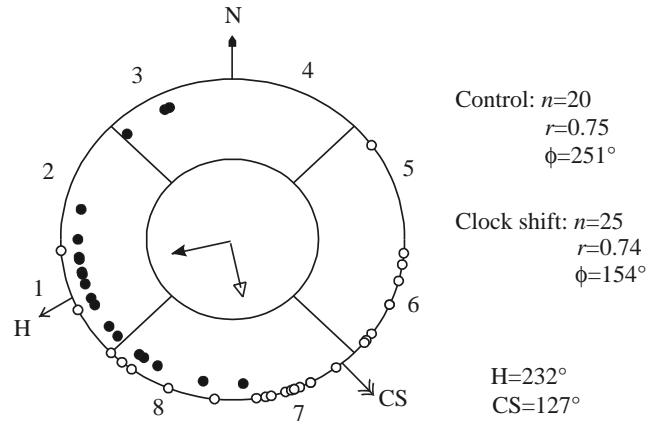r=0.74
ϕ=154°

H=232°
CS=127°

Fig. 1. Circular diagram of the vanishing bearings of the control (filled circles) and clock-shift (open circles) groups released 9.95 km from home in Oxford, UK. Birds were released individually and followed through binoculars until they vanished from sight. Bearings at vanishing were recorded for each bird. The mean bearings and vectors are shown in the diagram as the arrows in the inner circle (filled arrow, control; open arrow, clock shift). r is the mean vector length, and ϕ is the mean vanishing bearing. The edge of the inner circle represents a vector length of 1. The single-headed arrow represents the home direction (H), and the double-headed arrow represents the predicted home direction for clock-shifted birds (CS). Reproduced from Holland (1998).

compass. It should be noted, however, that if the birds are switching to the magnetic compass when clock-shifted, then this leads to the same prediction. The problems of interpretation of clock shift in the familiar area will be discussed in the next section.

The role of clock-shift experiments for visual landmark research

Clock-shift manipulations in the familiar area have been at the crux of research on the role of visual landmarks in pigeon homing, but the results of the many experiments have not led to a definite answer. In some cases, birds released at familiar sites have shown full deflection (Graue, 1963; Keeton, 1969; Füller et al., 1983; Luschi and Dall'Antonia, 1993). These experiments have been interpreted as showing that either landmarks are being used in a mosaic map or are not used at all. Indeed, in the case of Füller et al. (1983), the birds were released up to 60 times from the same site but still showed the full expected shift. In other cases, reduced or absent deflection has been shown, often when clock-shifted birds were made anosmic and thus could not use olfactory cues to navigate with the sun compass (Bingman and Ioalé, 1989; Wallraff et al., 1994; Gagliardo et al., 1999, 2002; Wiltschko and Wiltschko, 2001). These experiments have generally been interpreted as showing that the reduced deflection was caused by the influence of familiar visual landmarks independent of the map and compass system (although see Sandberg et al., 1999 for an explanation involving stress of multiple treatment, which is

certainly the case where both clock shift and anosmia are induced). Results of clock-shift experiments in the familiar area are thus open to several interpretations. Some support the theory that visual landmarks are independent of the map and compass (piloting) whilst others, since they result in deflection in the clock-shift direction, have to be interpreted as evidence that either the landmarks are used to give a compass bearing (mosaic map) or else are being ignored. There is no reason why they cannot use both mechanisms, as has been demonstrated in small-scale laboratory experiments (Kamil and Cheng, 2001). Indeed, several experiments involving clock shift of seed-caching birds have shown that, in general, landmarks are used in a mosaic map format (Wiltschko and Balda, 1989) but, like their large-scale counterparts, clock shift is often reduced or absent, leading to other non-sun compass-based interpretations (Duff et al., 1998; Wiltschko et al., 1999). One of the problems with interpreting the results of clock shift in the familiar area is that, in fact, results are rarely black and white. Fig. 2 shows the vanishing diagram of a group of clock-shifted birds released from a familiar site (taken from Holland, 1998). The birds have deflected from the home direction but not as much as expected. This could be interpreted as evidence that either (1) individual birds are compromising between the sun and magnetic compass and take a heading that is a compromise between the two possible directions or (2) that some individuals are choosing the sun compass direction and others are choosing the home direction, resulting in a mean vanishing bearing that is intermediate between the two. The noise inherent in the data from vanishing bearings makes it difficult to distinguish between these two interpretations, but two experiments in which clock-shifted birds were tracked demonstrated that both deflected and undeflected tracks were present, sometimes in the same release (Holland et al., 2000; Bonadona et al., 2000). This suggests that the intermediate bearing often seen in clock-shift releases in the familiar area results from the second possibility. The reasons for the two

different orientations within the same release is unclear but may be the result of differing degrees of familiarity between birds, the effect of the structure of the landscape, visibility of the loft or, as has been noted by Neuss and Wallraff (1988), previous clock-shift experience. However, after careful consideration of the available data, Wallraff et al. (1999) concluded that, despite the inherent variability, the results of familiar area clock-shift experiments demonstrated that as reduced deflection was only present at familiar sites, this indicated that birds could use landmarks for piloting.

Despite this, a recent experiment has called into question whether familiar area clock-shift experiments are evidence for the use of visual landmarks at all. It was noted in the previous section that a switch to the magnetic compass could also produce the pattern of results seen in familiar area clock-shift experiments. Wiltschko and Wiltschko (2001) have noted that in the case of these familiar area experiments, the role of visual landmarks has to be inferred, since neither vision nor the landmarks have been directly manipulated. They found evidence that there is less deflection in clock-shift experiments than expected at both familiar and unfamiliar places (Wiltschko et al., 1994; Chappell, 1997) and that by fixing magnets to clock-shifted pigeons, the full effect of the clock shift was restored. This suggests that reduced or absent deflection might be a consequence of compromise between the sun compass and magnetic compass. The results cannot explain all the reduced deflection from previous experiments, however. Bingman and Ioalé (1989) and Wallraff et al. (1994) both found different degrees of deflection depending on whether the birds were unfamiliar, familiar or familiar and anosmic when released from a site (although see Luschi and Dall'Antonia, 1993). It would be difficult to interpret these results in terms of simply compromise between the sun compass and the magnetic compass. Nevertheless, Wiltschko and Wiltschko (2001) provide an alternative explanation for the reduced deflection seen in clock-shift experiments. The results of clock-shift experiments alone do not constitute hard evidence that birds are using landmarks independent of the map and compass system.

Evidence from neurobiology: the role of the hippocampus

Numerous lesion studies have demonstrated that the hippocampus plays a role in spatial memory of birds and mammals (O'Keefe and Nadel, 1978; Bingman et al., 1998). Several experiments by Bingman and co-workers (Bingman et al., 1984, 1987; Bingman and Mench, 1990) involving release experiments with hippocampal-lesioned pigeons have demonstrated that the hippocampus is involved in memory for orientation from a familiar but not an unfamiliar area, and there is extensive evidence from laboratory tests that hippocampal lesions impair the ability of birds to use visual landmarks (Sherry and Vaccarino, 1989; White et al., 2002). Also, some recent experiments combining clock shift, anosmia and hippocampal lesions have demonstrated that the hippocampus plays a role in memory for non-sun compass-based orientation
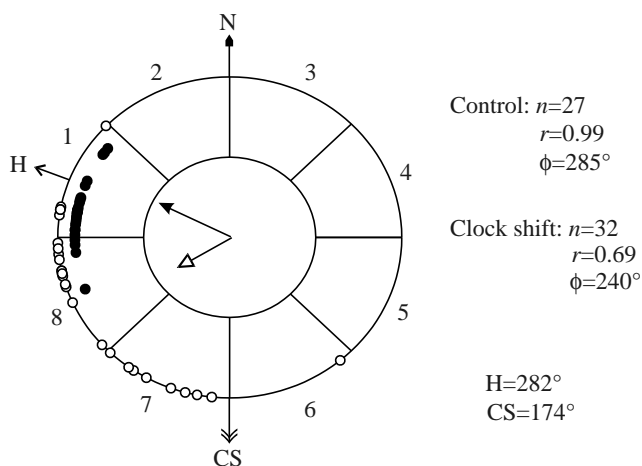
Fig. 2. Circular diagram of the vanishing bearings of the control (filled circles) and clock-shift (open circles) groups released 2.3 km from home in Oxford, UK. Methods and interpretation are as for Fig. 1. Reproduced from Holland (1998).

Control: *n*=27
r=0.99
φ=285°

Clock shift: *n*=32
r=0.69
φ=240°

H=282°
CS=174°

in the familiar area but not sun compass-based orientation (Gagliardo et al., 1999, 2002). Taken together, these experiments demonstrate that the hippocampus is the site of spatial memory for orientation mechanisms that are independent of the map and compass mechanism, but, just like the clock-shift experiments, they do not directly demonstrate that birds are using visual landmarks to navigate. Once again, their use is inferred. Despite the wealth of data showing that the hippocampus is involved in memory for visual landmarks in the laboratory, there has been resistance to applying the findings of small-scale laboratory experiments to wide-ranging homing. Wiltschko and Wiltschko (2003) note that in the former, all aspects of the problem, the location of the goal and the attendant cues, are within visual range of the animal, whereas in homing the goal is not in visual range and thus represents a different task. It seems then that lesion experiments demonstrate that the hippocampus of birds is involved in memory for orientation from familiar places, using a mechanism that is independent from the sun compass. However, they do not provide direct evidence that pigeons use visual landmarks for orientation. Whilst laboratory studies suggest that the hippocampus is involved in memory for visual cues, this small-scale task is different from a homing task and so caution should be taken when applying the results of these types of experiments to homing from distant sites.

Direct evidence for the use of visual landmarks by homing pigeons

No experiments described in this paper so far have demonstrated direct evidence for the use of visual landmarks in pigeon homing. Direct evidence would require either manipulation of the cue being investigated or the sense required to detect it. In the laboratory, direct evidence for landmark use can be obtained by shifting landmarks with a corresponding shift in the animal's behaviour. The nature of release experiments, however, makes this task very difficult. To date, no one has attempted to manipulate or move features of the landscape in a release experiment. Given the lack of control inherent in a field experiment, it is highly unlikely that even if one or two landmarks at a release site could be moved that this would result in a corresponding shift in orientation. Successful landmark shifts in the laboratory have required control of cues external to the experimental task in order to discount their use (see Jones and Kamil, 2001 for a description of such a task). It is possible, however, to manipulate the visual sense of pigeons and still perform release experiments. Schmidt-Koenig and Schlichte (1972) fitted frosted contact lenses that restricted vision to less than 6 m ahead of the bird without obscuring the ability to perceive the sun's disc. They found that birds could still orient successfully from a release site and were only handicapped in locating the home loft. A later version of the experiment in which birds were radio-tracked demonstrated that they could home to within 0.5 km of the home loft whilst wearing frosted lenses (Schmidt-Koenig and Walcott, 1978). More than anything else, these

experiments were responsible for the prevailing view for two decades that pigeons do not use visual landmarks for orientation from familiar places (Schmidt-Koenig, 1979). They are still cited today as evidence for this view (Walker et al., 2002). However, Baker (1984) has noted that in this type of experiment, if an animal can still perform the task when the sense has been removed, it is not evidence that they do not use the sense, only that they have other redundant systems that can be used in its absence. Two other experimental techniques have addressed this issue by comparing performance of birds with and without visual access to the landscape.

Braithwaite and co-workers (Braithwaite and Guilford, 1991; Braithwaite, 1993; Burt et al., 1997) demonstrated that if birds were allowed to preview the landscape from a clear Perspex box for 5 min before release, they homed significantly faster than when denied such a preview. The suggestion that the results are a consequence of some non-specific effect of the visual treatment (Wiltschko and Wiltschko, 2003) is countered by the fact that there is no effect of the preview at unfamiliar sites (Braithwaite and Newman, 1994). It has recently been identified that the difference in homing times occurs because birds denied a preview of the landscape travel more tortuous paths within the first 1000 m after release than those with access to the landscape prior to release (Biro et al., 2002). However, there is no effect of the preview above 7 km from the home loft and this has led to criticism of its relevance to longer-distance homing experiments (Wallraff et al., 1994).

Gagliardo et al. (2001) addressed this problem. They used an escape arena with walls that could be open to allow access to the visual landscape or closed. A bird could escape from the arena through hanging bars on the walls when released from a box at the centre. They set up the arena at familiar release sites (7 km, 12 km and 18 km from home) and compared the orientation of a group who could see the landscape on release with a group who couldn't. Both a control group and a group that were made anosmic were used. The anosmic group that was denied a view of the landscape on release was not oriented at the point of escape from the arena, whereas the control group was. This demonstrated that, in the absence of visual cues, the birds could use olfactory cues to orient, whilst when both visual and olfactory cues were absent, they could not orient. Anosmic birds with visual access were well oriented in the home direction at the point of escape and at vanishing, demonstrating that visual cues could be used to orient in the absence of olfactory cues. The non-visual anosmic birds were also oriented in the home direction at vanishing, demonstrating that once visual cues were made available upon escape from the arena these birds could orient. This shows that both visual cues and olfactory cues can be used to orient in the home direction at familiar sites: 'interchangeable roles', as Gagliardo et al. (2001) define it. The preview and the escape arena experiments provide direct evidence that homing pigeons use visual cues to navigate from familiar sites. However, they cannot distinguish between a mosaic map type mechanism and a piloting mechanism. Nevertheless, the technique used by Gagliardo et al. (1999) could be extended to include rotation

of the sun compass and magnetic compass. If anosmic birds that could see the landscape were oriented in the direction of compass rotation at their exit from the arena then this would indicate that they were using the visual cues as part of a mosaic map. If they were oriented in the home direction, however, this would indicate their use in a piloting mechanism.

The role of the visual sense of pigeons

Of great importance to the way pigeons use landmarks is how their visual field actually processes visual information. Pigeons and other ground-foraging birds are essentially myopic in the lower visual field (Erichsen et al., 1989). This is most likely an adaptation to foraging for food whilst being able to maintain an in-focus view of the horizon to scan for predators without needing to accommodate (Hodos and Erichsen, 1990). However, this means that, when in flight, the lower visual field is out of focus and pigeons can only maintain the panoramic view in focus. This has interesting implications for the use of visual landmarks, in that the pigeon is effectively restricted to using features of the horizon whilst in flight, whereas when on the ground it can use closer visual landmarks. This might suggest why it is harder to demonstrate a role for visual landmarks in homing than in foraging. It also explains why the best demonstrations that vision is involved in homing have the birds released from a box that is near the ground when they start, from which they can see the surrounding landscape. This is, in fact, a closer analogy to the natural behaviour of taking off after ground foraging than most homing releases, where the bird is removed from a box with no view of the landscape and tossed into the air immediately. It has been suggested that the use of horizon features would result in a mosaic map type representation of landmarks involving a compass (Chappell and Guilford, 1997) but, for obvious reasons, it is difficult to know what a pigeon needs to be able to bring into focus in order to navigate by it. A wood might be a blur, for example, but it would still be distinguishable from a corn field or a range of hills. Clearly, experiments are needed to further establish what pigeons can and cannot focus on when in flight, but this raises interesting possibilities. Coincidentally, most of the experiments in which pigeons demonstrate reduced clock shift at familiar sites were performed in places where large-scale terrain features, such as mountain ranges and the sea coast, were visible (Bingman and Ioalè, 1989; Gagliairdo et al., 1999; Bonadona et al., 2000), suggesting that the structure of the landscape might be a crucial factor in what mechanism is used.

Conclusions

The results of anosmia, hippocampal lesions and some clock-shift experiments (and sometimes a combination of all three) on homing of pigeons suggests that they have a mechanism of orientation that is not linked to the sun compass. However, piloting by visual landmarks as an explanation can only be inferred because neither the visual sense nor the landmarks themselves are manipulated. The recent experiment by Wiltschko and Wiltschko (2001) has suggested an alternative explanation for the reduced deflection often seen in familiar area clock-shift experiments and so caution must be used in its interpretation. Direct evidence for the use of visual landmarks by homing pigeons has been obtained using two experimental techniques, but neither type of experiment can distinguish between their use in a mosaic map or for piloting. Future experiments to test this would have to involve rotation or ablation of the sun compass and magnetic compass in combination with manipulation of visual access to the landscape. We know that homing pigeons and other birds can use visual landmarks both with a compass and independently to locate a goal in small-scale laboratory experiments (Kamil and Cheng, 2001). However, as considered in the previous section, the way the pigeon processes visual information in flight is different from when foraging. For this reason, understanding whether homing pigeons can use either mechanism or only one of them in a wide-ranging orientation problem, where the goal is out of sensory contact, is key to our understanding of how birds process visual information to represent space at all scales.

Until such time as the crucial experiments are performed, however, our knowledge of the role of visual landmarks in pigeon homing cannot stretch beyond the fact that they use them.

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