

White-throated sparrows calibrate their magnetic compass by polarized light cues during both autumn and spring migration

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SUMMARY

The interaction and hierarchy of celestial and magnetic compass cues used by migratory songbirds for orientation has long been the topic of an intense debate. We have previously shown that migratory Savannah sparrows, *Passerculus sandwichensis*, use polarized light cues near the horizon at sunrise and sunset to recalibrate their magnetic compass. Birds exposed to a ± 90 deg. shifted artificial polarization pattern at sunrise or sunset recalibrated their magnetic compass, but only when given full access to celestial cues, including polarized light cues near the horizon. In the current study, we carried out cue conflict experiments with white-throated sparrows, *Zonotrichia albicollis*, during both spring and autumn migration in a transition zone between the species' breeding and wintering areas on the south shore of Lake Ontario. We show that white-throated sparrows also recalibrate their magnetic compass by polarized light cues at sunrise and sunset. Sunrise exposure to an artificial polarization pattern shifted relative to the natural magnetic field or exposure to a shift of the magnetic field relative to the natural sky both led to recalibration of the magnetic compass, demonstrating that artificial polarizing filters do not create an anomalous, unnatural orientation response. Our results further indicate that there is no evidence for a difference in compass hierarchy between different phases of migration, confirming previous work showing that polarized light cues near the horizon at sunrise and sunset provide the primary calibration reference both in the beginning and at the end of migration.

Key words: orientation, magnetic compass, compass calibration, birds.

INTRODUCTION

Migratory songbirds use directional cues from the sun, stars and the magnetic field to determine their migratory direction (Sauer, 1957; Wiltschko and Wiltschko, 1972; Emlen, 1975; Able, 1982; Moore, 1987; Moore and Phillips, 1988; Schmidt-Koenig, 1990). Because of the changing relationship between magnetic and geographic North, birds need to calibrate the different compass systems with respect to each other on a regular basis to prevent navigational errors (Muheim et al., 2006b; Muheim et al., 2007). How and when birds calibrate their compasses and which compass system has priority over the others have been topics of an intense debate over the past decades, resulting in a large body of research on cue conflicts between magnetic and celestial references. In a review of the cue conflict literature (Muheim et al., 2006a) we found that birds regularly recalibrate their magnetic compass using polarized light cues from the sky near the horizon at sunset (and sunrise). Apparent inconsistencies in the cue hierarchies (i.e. magnetic field, stars, sun, polarized light pattern) used by birds during the premigratory and migratory periods reported by earlier investigators can be explained by differences in access to cues near the horizon during exposure to the cue conflict, rather than the age of the birds or the season of the year (Muheim et al., 2006a). We confirmed our hypothesis in experiments carried out with migratory Savannah sparrows, *Passerculus sandwichensis*, and showed that they use polarized light cues at sunrise and sunset to recalibrate their magnetic compass (Muheim et al., 2006b). Birds exposed to a ± 90 deg. shifted artificial polarization pattern at sunrise or sunset recalibrated their magnetic compass, but only when given full access

to celestial cues, including polarized light cues near the horizon (Muheim et al., 2006b). The birds did not recalibrate their magnetic compass when the view of the sky near the horizon was blocked during exposure or when the exposure took place at solar noon (Muheim et al., 2007).

An unsuccessful attempt to repeat our findings with Australian silvereyes, *Zosterops lateralis*, led to the suggestion that one or more of the following biologically relevant factors may explain the disparate results between studies (Wiltschko et al., 2008) (but see Muheim et al., 2008): (a) calibration of compasses and compass hierarchy may be species specific, (b) compass calibration may depend on phase of migration (e.g. spring vs autumn, beginning vs end of migration), or (c) regional variation in the relationship of magnetic and celestial cues (such as differences between Australia and North America) may affect the calibration process. Also, Wiltschko et al. (Wiltschko et al., 2008) proposed that specific experimental methods may produce disparate results; in particular, cue conflicts produced by artificially shifting the polarization pattern with polarizing filters relative to the natural geomagnetic field may produce different results than cue conflicts produced by shifting the magnetic field relative to natural celestial cues.

Here we report the results of experiments in which we addressed some of these concerns. We carried out cue conflict experiments with white-throated sparrows, *Zonotrichia albicollis* Gmelin, during spring and autumn migration in a transition zone between their breeding and wintering areas on the south shore of Lake Ontario to answer the following questions.

(1) Do white-throated sparrows recalibrate their magnetic compass by polarized light cues at sunrise and sunset as previously observed in Savannah sparrows? Besides Savannah sparrows (Bingman, 1983; Able and Able, 1990; Able and Able, 1993; Able and Able, 1995a; Muheim et al., 2006b; Muheim et al., 2007), recalibration of the magnetic compass has previously been shown in pied flycatchers, *Ficedula hypoleuca* (Prinz and Wiltshko, 1992; Weindler and Liepa, 1999) and Swainson's and gray-cheeked thrushes, *Catharus ustulatus* and *Catharus minimus* (Cochran et al., 2004). Moreover, pied flycatchers (Bingman, 1984) and Savannah sparrows (Able and Able, 1997) tested under natural celestial cues in a vertical magnetic field after exposure to a shifted magnetic field had not recalibrated their celestial compasses, indicating a recalibration of the magnetic compass instead. With white-throated sparrows, we tested a bird species that had not previously been studied in these types of cue conflict experiments.

(2) Does exposure to an artificial polarization pattern shifted relative to the natural magnetic field lead to the same response as horizontal rotation of the magnetic field relative to the natural sky? Wiltshko et al. (Wiltshko et al., 2008) suggested that the use of artificial polarizers to shift the relationship between magnetic and polarized light cues creates unnatural conditions that can lead to responses that do not reflect the natural behavior of the birds (but see Muheim et al., 2008). To test whether there is a difference in the response to these two experimental treatments, we exposed sparrows during autumn migration to either a +90 deg. shifted magnetic field or a ± 90 deg. shifted polarization pattern around sunrise.

(3) Is there a difference in compass hierarchy between different phases of migration? Wiltshko et al. (Wiltshko et al., 2008) argued

that phase of migration (e.g. spring vs autumn, beginning vs end of migration) could be a potential factor influencing whether birds recalibrate their magnetic compass or the celestial compasses (but see Muheim et al., 2008). It is undisputed that the magnetic compass is recalibrated by celestial cues during the premigratory period, i.e. before the start of a migration. However, the difficulty of determining the precise onset of migration in some species or at some locations can make it difficult to determine the reasons for an observed recalibration of the magnetic compass, especially in what is presumed to be the early stage of migration (Wiltshko et al., 2008) (but see Muheim et al., 2008). The cue conflict experiments carried out with white-throated sparrows in the present study during both spring and autumn migration likely tested the responses of birds in different migratory phases, because the study site was located at the transition between breeding and wintering areas of white-throated sparrows (Falls and Kopachena, 1994).

METHODS

Study species and orientation experiments

Juvenile and adult white-throated sparrows were captured at Braddock Bay Bird Observatory (43 deg. 19'N, 77 deg. 43'W; total intensity of the geomagnetic field: $\sim 54,500$ nT; inclination: 70.5 deg.; declination: -12 deg.) on the south shore of Lake Ontario during spring (end of April–beginning of May 2007) and autumn migration (mid September–mid October 2006–2008). The species is a short- to medium-distance temperate migrant, breeds across southern and central Canada and throughout the Great Lakes region, and winters in the southern and eastern United States (Falls and Kopachena, 1994). Each bird was aged by plumage (such as the shape and wear of the rectrices and primaries) and in the

Table 1. Orientation of migratory white-throated sparrows exposed to a +90 deg. shifted magnetic field at sunrise (M90SR) during autumn migration 2006–2008 at Braddock Bay Bird Observatory

Bird	Age	Control orientation (deg. mN)	Orientation after exposure to M90SR (deg. mN)	Individual response (deg.)
108	Juv	190	140	310
115	Ad	60	160	100
117	Juv	105	185	80
119	Juv	310	65	115
125	Juv	335	265	290
126	Juv	160	345	185
127	Juv	280	175	255
128	Juv	75	300	225
131	Juv	170	290	120
134	Juv	55	130	75
135	Juv	170	290	120
141	Juv	345	50	65
145	Juv	0	115	115
147	Juv	25	270	245
703	Juv	320	280	320
704	Ad	325	40	75
724	Juv	150	125	335
725	Juv	170	80	270
726	Juv	335	95	120
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<i>N</i>		19	19	19
α		339.5 deg. ax	110.4 deg. ax	100.4 deg. ax
<i>r</i>		0.394	0.341	0.489
<i>P</i>		0.05	0.11	0.009

For each bird, age (Juv: juvenile, Ad: adult), control orientation (relative to magnetic North, mN), orientation after the exposure (relative to magnetic North) and the response of each individual to the exposure (orientation after exposure – orientation before exposure, i.e. control orientation set to 0 deg.) is given. For each experimental treatment, the number of birds (*N*), mean direction (α), mean vector length (*r*) and the *P*-value according to the Rayleigh test are given. ax: axial distribution. For illustration see Fig. 1A.

autumn by the degree of skull pneumatization and the color of the iris (Pyle, 1997).

The sparrows were kept in cages in groups of 2–3 individuals for a maximum of 10 days and fed with seeds (millet, nyjer, sunflower), fish pellets and water *ad libitum*. The holding room had windows covered with translucent plastic on all four walls, so that the birds were exposed to the natural light regime, but could not detect celestial compass cues (polarized light, sun position).

Orientation was assessed in modified Emlen funnels (Emlen and Emlen, 1966) lined with type-writer correction paper (BIC, GmbH, Eschborn, Germany) and covered with a translucent Plexiglas sheet to guarantee that the birds could only use their magnetic compass for orientation. All experiments took place indoors in a uniformly lit shed (for more details, see Deutschlander and Muheim, 2009).

Experimental procedures and manipulations

Experiments started once a bird reached a fat score of at least 3 (with two exceptions where the birds had a fat score of only 2) according to the scale by Helms and Drury (Helms and Drury, 1960) to guarantee that we tested only birds in migratory disposition (cf. Deutschlander and Muheim, 2009). All birds were first tested for control orientation without prior exposure to outside cues between capture and experiment. Once a bird exhibited directed orientation in the control experiment (for criteria see below), it was exposed for 60 min to one of the experimental cue conflicts described below and then tested again on the same or the following evening for magnetic orientation. Birds that were either not active or not well oriented (see below) were tested again, but not more than three times in total. All birds were released at the end of the experiments.

Exposure to +90 deg. shifted magnetic field at sunrise (M90SR): the +90 deg. artificially shifted magnetic field (i.e. magnetic N=geographic E) was produced by a doubly-wrapped cube-surface (Merritt) coil set up in an open field surrounded by trees. During exposure, the birds were held in groups of 2–5 in a cage (42×42×35 cm) made of plastic and wood with a window on each

of the four sides, providing an unobstructed view of the natural sky near the horizon. Exposures lasted from 30 min before to 30 min after local sunrise.

Exposure to ±90 deg. shifted polarization pattern at sunrise (P90SR) or sunset (P90SS): exposures were carried out in a wooden box (77×77×50 cm) set up about 30 m from the coil used for the magnetic field exposures. The windows (28×28 cm) on each side of the square box were covered with one depolarizing and one polarizing filter, so that incoming light was first depolarized and then either horizontally or vertically polarized. Two vertically and two horizontally aligned polarizing filters were placed on opposite sides along the same axis (vertically aligned filters were placed in windows 180 deg. apart on one axis and the horizontally aligned filters 180 deg. degrees apart on the perpendicular axis), creating an artificial polarization pattern visible to the birds in the box that simulated the natural polarization at sunrise and sunset. The box was aligned so that the polarization axis was shifted ±90 deg. relative to the natural polarization axis. During exposure, the birds were held in groups of 2–5 in the same type of cage used in the magnetic field shifts, which was placed in the center of the wooden box with the polarizing filters, providing the birds an unobstructed view of the horizon during the exposure. Exposure to the artificial polarization pattern lasted from 30 min before to 30 min after local sunrise.

Data analysis

The type-writer correction papers were analyzed with a visual estimation method (cf. Mouritsen and Larsen, 1998) [see supporting online material in Muheim et al. (Muheim et al., 2006b)] by a person blind to the experimental condition and the North mark. Each paper was given a score for activity from 0 (0–50 scratches) to 4 (>2000 scratches) and a score for estimation accuracy from 0 (>45 deg. estimated difference between different observers) to 4 (0–5 deg. difference). Papers with activity=0, concentration=0 or total score (activity + concentration) <3 were excluded, so that only experiments with well-directed orientation were included in further analysis.

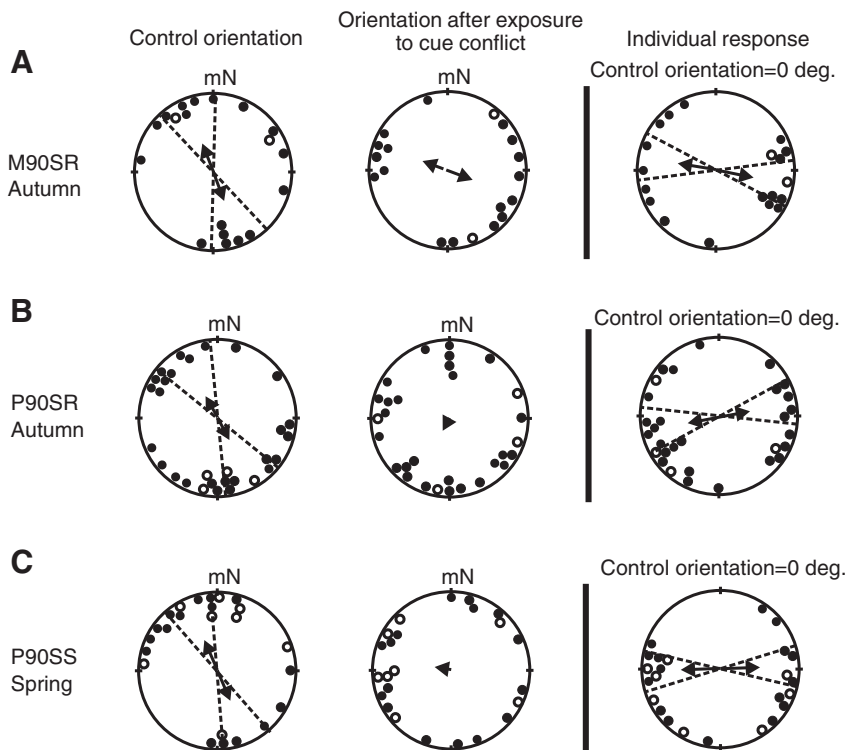


Fig. 1. Orientation of migratory white-throated sparrows tested during autumn migration 2006–2008 and spring migration 2007 at Braddock Bay Bird Observatory. (A) Exposure to a +90 deg. shifted magnetic field at sunrise (M90SR); (B) exposure to a ±90 deg. shifted artificial polarization pattern at sunrise (P90SR); (C) exposure to a ±90 deg. shifted artificial polarization pattern at sunset (P90SS). Left panels: control orientation of the birds prior to the exposure; middle panels: orientation after exposure to the cue conflict; right panels: individual responses or change in each bird's orientation after exposure to the cue conflict. The left and middle panels give the absolute orientation relative to magnetic North=0 deg., the right panels show the change in orientation of individual birds as a result of the exposure (orientation after exposure – orientation before exposure, i.e. control orientation set to 0 deg.). Each data point in the circular diagrams shows the magnetic orientation of an individual bird; juveniles are shown as filled and adults as open circles. Each arrow gives the mean orientation of the group of birds (α). The length of each arrow is a measure of the concentration (r) of the group drawn relative to the radius of the circle=1. Double-headed arrows indicate axially distributed samples. Broken lines give the 95% confidence interval for the mean bearing or mean axis for significantly directed samples (Batschelet, 1981). For more details see Tables 1–3.

We used circular statistics to test whether a group of birds was significantly directed (Rayleigh test) (Batschelet, 1981), and the method of doubling the angles to test whether a group was axially distributed ($r_{axial} > r_{unimodal}$). As we were interested in the difference of the response of each individual bird to the exposure, we calculated the difference between each individual's control direction and the direction chosen after the exposure. The 95% confidence intervals were used to examine whether the observed difference included the expected shift. Differences between two groups were tested with the non-parametric circular Watson U^2 test, and differences between three groups with the non-parametric circular Mardia–Watson–Wheeler test (Batschelet, 1981).

RESULTS

Autumn experiments

Both groups of white-throated sparrows oriented axially towards SSE–NNW in the control experiments (Fig. 1A,B left panel, Tables 1 and 2) and did not significantly differ from each other (Watson U^2 : $U^2=0.11$, $P>0.2$, d.f.=19, 30). The control orientation of adult birds ($N=6$) was indistinguishable from that of the juvenile birds ($N=43$) (Watson U^2 : $U^2=0.18$, $P>0.05$, d.f.=6, 43).

After exposure to a +90 deg. shifted magnetic field at sunrise (M90SR), individual birds shifted their magnetic orientation by approximately ± 90 deg. relative to their control orientation

(Fig. 1A right panel, Table 1). Similarly, after exposure to a ± 90 deg. shifted polarization pattern at sunrise (P90SR), individual birds shifted their orientation by about ± 90 deg. relative to their control orientation (Fig. 1B right panel, Table 2). In both treatments, the resulting distribution of bearings after exposure was not significantly oriented relative to magnetic North; thus, the birds did not show a consistent orientation relative to magnetic North as a group (Fig. 1A,B middle panel, Tables 1 and 2). However, the change in the direction of individual birds after the experimental treatments was highly consistent. Individual responses to a ± 90 deg. shift in polarization were indistinguishable from the individual responses to a +90 deg. shift in the magnetic field (Watson U^2 : $U^2=0.04$, $P>0.5$, d.f.=19, 30; Fig. 1A,B right panels). Also, there was no difference in the response of juvenile and adult birds to the experimental treatments (Watson U^2 : $U^2=0.03$, $P>0.5$, d.f.=6, 43).

Spring experiments

During spring migration, mean control orientation was directed along the NNW–SSE axis (Fig. 1C left panel, Table 3). Individual birds exhibited a consistent ± 90 deg. shift relative to their direction of orientation prior to exposure, indicating that the birds had recalibrated their magnetic compass (Fig. 1C right panel, Table 3). As during autumn, they did not show a consistent direction of

Table 2. Orientation of migratory white-throated sparrows exposed to a ± 90 deg. shifted artificial polarization pattern at sunrise (P90SR) during autumn migration 2006 and 2007 at Braddock Bay Bird Observatory

Bird	Age	Control orientation (deg. mN)	Orientation after exposure to P90SR (deg. mN)	Individual response (deg.)
63	Juv	335	285	310
66	Juv	95	180	85
68	Juv	315	135	180
70	Juv	170	155	345
71	Juv	135	225	90
78	Juv	15	220	205
82	Juv	350	275	285
88	Juv	185	35	210
89	Juv	100	360	260
90	Juv	105	220	115
94	Juv	130	360	230
95	Juv	170	300	130
112	Juv	180	285	45
118	Juv	230	125	235
122	Juv	310	215	235
132	Ad	170	110	265
138	Juv	215	170	65
140	Ad	330	190	105
142	Juv	55	130	255
144	Juv	125	0	265
148	Juv	205	90	300
162	Juv	165	290	315
166	Ad	190	70	220
172	Ad	150	270	75
173	Juv	190	255	235
668	Juv	295	340	245
670	Juv	245	120	125
671	Juv	305	180	240
674	Juv	295	200	120
697	Juv	300	5	65
<i>N</i>		30	30	30
α		151.8 deg. ax	213.0 deg.	78.9 deg. ax
<i>r</i>		0.315	0.173	0.401
<i>P</i>		0.05	0.410	0.007

For detailed explanation see Table 1. For illustration see Fig. 1B.

orientation relative to magnetic North after exposure (Fig. 1C middle panel). Adult ($N=8$) birds did not differ from juveniles ($N=16$) in their control orientation, in the orientation after exposure to the cue conflict or in the change in orientation before and after the exposure (Watson U^2 : all $P>0.2$). The individual responses to the cue conflict during spring at sunset did not significantly differ from the responses during autumn at sunrise or sunset (Mardia–Watson–Wheeler test: $W=2.15$, $P=0.7$).

DISCUSSION

White-throated sparrows recalibrate their magnetic compass by polarized light cues near the horizon at sunrise and sunset, as previously observed in Savannah sparrows

The present experiments were carried out with a species not previously tested in cue conflict experiments. With white-throated sparrow we add another species to the list of birds that show recalibration of the magnetic compass after exposure to a cue conflict between celestial polarized light cues near the horizon and magnetic cues (see Muheim et al., 2006a). The individual birds did not show a consistent magnetic orientation after exposure to the cue conflict (Fig. 1, middle panels), demonstrating that they did not show a simple alignment behavior (e.g. alignment of the magnetic compass along the artificial polarization axis during exposure) but that they truly recalibrated their magnetic compass as evident from their individual responses (Fig. 1, right panels).

As already observed in the closely related Savannah sparrows, both the control orientation and the response to the treatments were axial (e.g. Able and Able, 1990; Able and Able, 1993; Able and Able, 1995a; Muheim et al., 2006b; Muheim et al., 2007). In earlier

experiments we showed that only white-throated sparrows with fat scores of ≥ 3 exhibited seasonally appropriate migratory orientation (Deutschlander and Muheim, 2009). The axiality of the current control data cannot be explained by the fat level, but may have resulted from differences in experimental setup. In the earlier experiments, the birds were tested on the day of capture and were exposed for one hour to natural sunset cues just prior to the orientation experiments (Deutschlander and Muheim, 2009). In the present experiments, the birds were held for up to 5 days before testing started. Furthermore, the birds were deprived of access to natural celestial cues between capture and control experiments. Similar consistent axial magnetic control orientation in indoor experiments had previously been observed in Savannah sparrows (e.g. Able and Able, 1990; Able and Able, 1993; Able and Able, 1995a; Muheim et al., 2006b; Muheim et al., 2007); the exact reasons for this behavior are still unclear.

An axial response to the experimental treatment was expected after we manipulated the polarized light, because of the axial characteristics of the cue itself (cf. Brines, 1980; Brines and Gould, 1982). The ± 90 deg. shift of the polarization pattern can be interpreted by individual birds as either a $+90$ deg. or a -90 deg. shift, resulting in an axial distribution of the overall responses. By contrast, the expected orientation after recalibration of the magnetic compass as a result of the exposure to a $+90$ deg. shifted magnetic field was a unimodal -90 deg. shift in orientation compared with the control orientation. The axial response here was unexpected, but could have occurred for the same reasons as the axial control orientation and/or may indicate that some of the individuals may have been ambivalent in their directional preference.

Table 3. Orientation of migratory white-throated sparrows exposed to a ± 90 deg. shifted artificial polarization pattern at sunset (P90SS) during spring migration 2007 at Braddock Bay Bird Observatory

Bird	Age	Control orientation (deg. mN)	Orientation after exposure to P90SS (deg. mN)	Individual response (deg.)
2	Ad	70	315	245
3	Ad	330	115	145
4	Juv	15	295	280
5	Ad	20	300	280
6	Juv	175	290	115
9	Juv	355	130	135
11	Ad	20	230	210
17	Juv	285	160	235
18	Juv	275	105	190
20	Ad	355	265	270
28	Ad	295	45	110
31	Juv	325	15	50
32	Juv	140	240	100
33	Juv	305	20	75
34	Juv	120	40	280
35	Ad	175	270	95
36	Juv	310	175	225
39	Ad	360	265	265
42	Juv	165	200	35
43	Juv	90	0	270
47	Juv	185	305	120
49	Juv	320	250	290
51	Juv	355	255	260
96	Juv	345	65	80
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<i>N</i>		24	24	24
α		336.9 deg.ax	283.3 deg.	268.1 deg.ax
<i>r</i>		0.42	0.22	0.51
<i>P</i>		0.013	0.309	0.001

For detailed explanation see Table 1. For illustration see Fig. 1C.

Despite the axial orientation of our sparrows, the present experiments clearly show that white-throated sparrows recalibrate their magnetic compass after exposure to conflicting magnetic and polarized light cues near the horizon, as previously observed in Savannah sparrows (Muheim et al., 2006b; Muheim et al., 2007).

Sunrise exposure to an artificial polarization pattern shifted relative to the natural magnetic field and an exposure to a shift of the magnetic field relative to the natural sky both lead to a recalibration of the magnetic compass

Both a shift of an artificial polarization pattern relative to the natural magnetic field and a shift of the magnetic field relative to the natural polarization pattern led to a recalibration of the magnetic compass in white-throated sparrows. Recalibration of the magnetic compass as a consequence of exposure to a ± 90 deg. shift in the polarization pattern relative to the natural magnetic field confirms the findings from our previous experiments with Savannah sparrows (Muheim et al., 2006b; Muheim et al., 2007). Recalibration of the magnetic compass as a consequence of exposure to a shifted magnetic field relative to the natural polarization pattern is in agreement with previous results from Savannah sparrows (e.g. Able and Able, 1995a) and *Catharus* thrushes (Cochran et al., 2004).

Our results demonstrate that there is no methodological difference between a shift of an artificial polarization pattern relative to the natural magnetic field and a shift of the magnetic field relative to the natural polarization pattern. Thus, contrary to the arguments by Wiltschko et al. (Wiltschko et al., 2008), the artificial polarizers do not create an experimental condition that leads to unnatural behavior in the birds. The response of birds exposed to an artificially shifted polarization pattern can not be attributed to a fixed (i.e. parallel) alignment relative to the artificial polarization axis nor to a bias produced by the unnaturally high degree of polarization of the filters [around 99%, in contrast to an average of ~ 60 – 75% , with a maximum of up to 85%, observed in nature under clear skies (Cronin et al., 2006)]. Previous cue conflict studies using artificial polarizers tested the birds' orientation in funnels covered with artificial polarizers aligned to produce a 90 deg. shifted polarization axis, which led to fixed-axis orientation parallel to the e-vector axis of the polarization filters (e.g. Moore, 1986; Able and Able, 1995b). In our experiments, we assessed orientation after exposure to the cue conflict, rather than during the cue conflict, which resulted in a reorientation relative to the magnetic field by an amount corresponding to the difference between the natural and rotated polarization pattern (Muheim et al., 2006b; Muheim et al., 2007; Muheim et al., 2008).

There is no evidence for a difference in compass hierarchy between different phases of migration in sparrows

The present study demonstrates that white-throated sparrows use polarized light cues near the horizon at sunrise and sunset to recalibrate their magnetic compass during both spring and autumn migration. The white-throated sparrows recalibrated their magnetic compass both in the beginning of migration in autumn and at the end of migration in spring, when leaving and approaching the breeding area, respectively. These results support our earlier findings in Savannah sparrows, i.e. that birds recalibrate their magnetic compass when exposed to a polarization pattern artificially shifted relative to natural magnetic cues at sunrise and/or sunset (Muheim et al., 2006b; Muheim et al., 2007), as well as earlier studies demonstrating recalibration of the magnetic compass in response to a cue conflict between natural celestial and magnetic cues (Able and Able 1990; Able and Able, 1993; Able and Able, 1995a; Prinz

and Wiltschko, 1992; Bingman, 1993; Weindler and Liepa, 1999; Cochran et al., 2004; for review see Muheim et al., 2006a). In addition, the findings of the present study also support earlier observations (Able and Able, 1995a) and the findings from our review (Muheim et al., 2006a) that both juvenile and adult birds recalibrate their magnetic compass during both spring and autumn migration. Thus, a difference in compass hierarchy between different phases of migration (spring vs autumn, beginning vs end of migration) is unlikely to be the factor explaining the differences in responses observed between studies (Muheim et al., 2008).

CONCLUSIONS

The present results provide a further step in understanding the interaction and hierarchy of celestial and magnetic compass cues used by migratory songbirds for orientation during migration. We show that white-throated sparrows recalibrate their magnetic compass by polarized light cues near the horizon when exposed to a cue conflict. Even though the list of bird species exposed to a cue conflict with a full view of the horizon and reporting magnetic compass calibration includes both North American and European species, it will be important to test further species from a variety of geographical regions. The recalibration of the magnetic compass observed in the white-throated sparrows during both spring and autumn migration support previous findings that there is no evidence for a difference in compass hierarchy between different phases of migration (Muheim et al., 2006b). Our study thus provides further indication that polarized light cues near the horizon at sunrise and sunset provide the primary calibration reference both before and during migration. Additional experiments during different phases of migration will be important to further test this hypothesis. Last, but not least, we show that artifacts produced by the artificial polarizing filters cannot explain our earlier findings (Muheim et al., 2006b; Muheim et al., 2007), because cue conflicts created with artificial polarizers lead to recalibration of the magnetic compass similar to cue conflicts created by magnetic field shifts.

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