

## Report

# Marine Turtles Use Geomagnetic Cues during Open-Sea Homing

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## Summary

Marine turtles are renowned long-distance navigators, able to reach remote targets in the oceanic environment; yet the sensory cues and navigational mechanisms they employ remain unclear [1–3]. Recent arena experiments indicated an involvement of magnetic cues in juvenile turtles' homing ability after simulated displacements [4, 5], but the actual role of geomagnetic information in guiding turtles navigating in their natural environment has remained beyond the reach of experimental investigations. In the present

experiment, twenty satellite-tracked green turtles (*Chelonia mydas*) were transported to four open-sea release sites 100–120 km from their nesting beach on Mayotte island in the Mozambique Channel; 13 of them had magnets attached to their head [6] either during the outward journey or during the homing trip. All but one turtle safely returned to Mayotte to complete their egg-laying cycle, albeit with indirect routes, and showed a general inability to take into account the deflecting action of ocean currents as estimated through remote-sensing oceanographic measurements [7]. Magnetically treated turtles displayed a significant lengthening of their homing paths with respect to controls, either when treated during transportation or when treated during homing. These findings represent the first field evidence for the involvement of geomagnetic cues in sea-turtle navigation.

## Results and Discussion

Experimental displacements constitute one useful approach to investigating animal navigation systems [2, 8]. An animal translocated away from a site to which it is faithful (e.g., a breeding site) will most likely attempt to return to it, thus allowing the study of its navigational abilities in the field. In marine turtles, females typically display a strong fidelity to their nesting beach, where they faithfully return every few years from their residential feeding grounds, often located hundreds of kilometres away [9, 10]. Within a reproductive season, each turtle lays multiple clutches of eggs and remains in the waters close to the nesting beach between successive egg-laying events [9]. Previous homing experiments showed that, when experimentally translocated early during their reproductive period, turtles tend to return to their nesting beach to complete their seasonal egg-laying cycle [7, 11–16]. We employed this type of experiment to investigate the role of magnetic information in the homing abilities of green turtles nesting at Mayotte, the easternmost island of the Comoros archipelago in the Northern Mozambique Channel.

Turtles were captured while ashore to nest at Saziley beach (12.98°S; 45.19°E), in the southeastern part of Mayotte, and were then translocated to four release sites northeast, southwest, and southeast of Saziley (see Table S1 in the Supplemental Data available online). Five releases of four turtles each were performed (Table 1), with three different treatments: turtles magnetically disturbed only during transportation to the release site (MT group, n = 6), turtles magnetically treated during the homing trip (MH group, n = 7), and controls (C group, n = 7). Magnetically disturbed turtles had powerful, mobile magnets attached to their head (Figure 1A) to induce a randomly varying magnetic field around it [17]. Magnets were attached at the nesting beach (MT turtles) or on board just before release (MH turtles). MH turtles were therefore prevented from detecting geomagnetic cues during the homing process, whereas MT turtles

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Table 1. Homing Performances of the Three Turtle Groups

Turtle (CCL, cm)	Release (Direction)	Length of Homing Trip (km)	Speed of Homing Trip (km/d)	Straightness Index of Track Path	Straightness Index of Motor Path
<b>C GROUP</b>					
C1 (104)	1 (SW)	310	29.9	0.34	0.35
C2 (117)	1 (SW)	214	41.4	0.39	0.59
C3 (115)	2 (NE)	90	50.0	0.69	0.72
C4 (103)	2 (NE)	116	43.7	0.58	0.85
C5 (110)	3 (SE)	385	10.6	0.19	0.44
C6 (107)	4 (SE)	348	26.5	0.28	0.42
C7 (102)	5 (SE)	334	14.1	0.26	0.71
Mean ± SEM		257 ± 44	30.9 ± 5.7	0.39 ± 0.07	0.58 ± 0.07
<b>MH GROUP</b>					
MH1 (103)	1 (SW)	397	17.2	0.19	0.08
MH2 (109)	1 (SW)	—	—	−0.26	−0.18
MH3 (111)	2 (NE)	285	17.0	0.24	0.54
MH4 (107)	2 (NE)	97	67.4	0.65	0.72
MH5 (95)	4 (SE)	1435	6.8	0.05	0.03
MH6 (107)	4 (SE)	400	29.4	0.24	0.34
MH7 (108)	4 (SE)	492	27.1	0.19	0.25
Mean ± SEM		518 ± 192	27.5 ± 8.1	0.19 ± 0.10	0.25 ± 0.12
<b>MT GROUP</b>					
MT1 (110)	3 (SE)	763	7.2	0.08	0.25
MT2 (106)	3 (SE)	914	8.2	0.07	0.00
MT3 (105)	3 (SE)	371	19.5	0.19	0.35
MT4 (102)	5 (SE)	2214	4.4	0.04	0.05
MT5 (108)	5 (SE)	691	15.3	0.12	0.05
MT6 (112)	5 (SE)	861	18.5	0.11	0.09
Mean ± SEM		969 ± 261	12.2 ± 2.6	0.10 ± 0.02	0.13 ± 0.06

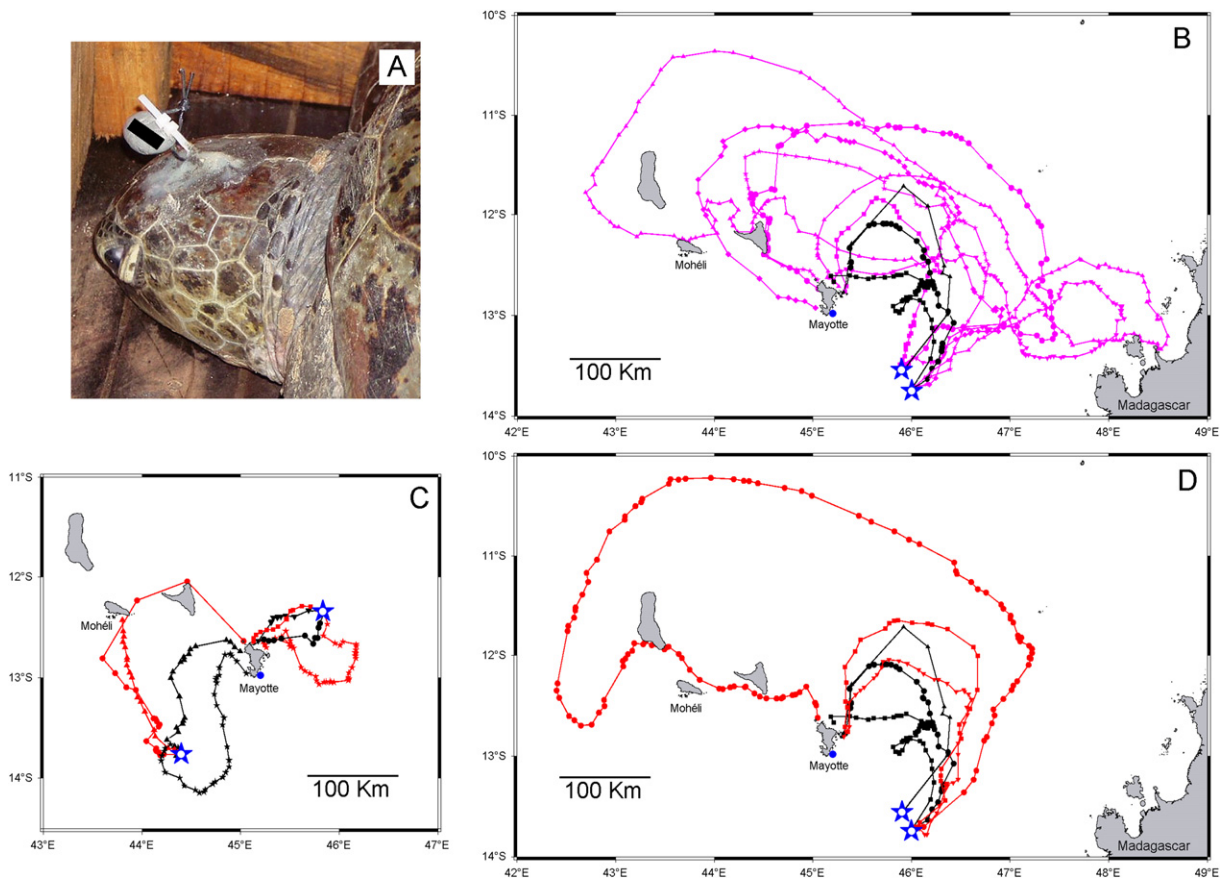
CCL = Curved Carapace Length. For turtle MH2, which stopped at Mohéli Island, homing-trip length and speed could not be calculated. See text for further explanations.

were made unable to collect these cues during transportation. In this way, we investigated the relative importance of geomagnetic cues detected during transportation and during homing and aimed to assess the role of alternative navigational strategies potentially exploitable by homing turtles. If turtles were relying on a “magnetic map” to fix their position with respect to home (by comparing magnetic parameters detected at the release site with those memorized at the nesting beach [3, 8]), we expected that MH turtles only would have been affected by the treatment. If turtles paid attention to magnetic cues picked up en route (e.g., to monitor the direction of passive displacement), or if magnets produce some long-lasting after-effect on magnetic receptors, then MT turtles would have exhibited an impairment in homing.

All displaced turtles but one returned to Mayotte in 2–29 days, with 18 of them later returning to Saziley beach. The only turtle that did not home (MH2) reached the coastal waters of Mohéli (another Comoros island 140 km westward of Mayotte) by following a straight path (Figure 1C) and remained there for the rest of the tracking period (83 days). Green turtles are known to frequent Mohéli, either to feed in its coastal waters or to breed in its beaches [18], but it is unknown whether turtle MH2 nested there. Most homing routes were not immediately directed toward Mayotte, with turtles often exhibiting curved or looping paths before reaching their target (Figures 1B–1D). The majority of turtles approached the island from the northern quadrants, as is especially evident for the releases from the southeast.

We first compared the homing performances of the three treatments by relying on track straightness index, which best represents the orientation efficiency of tracked paths [19]. A one-way ANOVA revealed a significant ( $F = 3.82$ ,  $p = 0.04$ ) difference among the indexes of the three groups, and a post-hoc Tukey test showed that controls had a significantly ( $p < 0.05$ ) higher mean index than the MT group but not the MH group, with no significant difference between magnetically treated groups. However, these straightness indexes, being directly derived from recorded tracks, do not take into account the possible deflecting action of ocean currents. They may consequently be unreliable if turtles do not compensate for current drift (i.e., if they are unable to anticipate the drift effects by adopting a heading that, albeit not immediately directed toward home, results in a movement leading to home with a shorter route when combined with drift action [20]). Such an inability has actually been suggested by a pilot study conducted on three green turtles displaced from their breeding sites at Europa Island (southern Mozambique Channel [7]). It is worth noting that, in any case, homing turtles are assumed to have been able to correct for passive displacements (including current drift and the initial displacement by boat) by estimating the home direction along their homing journey. Their possible ability to compensate for the current drift is another, independent question (see [7] for a detailed discussion of this complex matter).

To properly evaluate the turtles’ homing abilities, we therefore estimated the ocean surface currents in the



**Figure 1. Routes of Turtles Displaced from Their Nesting Beach as Reconstructed by Satellite Telemetry**

(A) Magnet attachment on a turtle's head. Disk-shaped magnets (18 mm diameter; 5 mm height) were incorporated with a cable tie in an oval-shaped body (gray colored) made of a fast-setting epoxy resin. This cable tie was connected to a second one linked to a third cable tie glued to the turtle's skin with a two-component epoxy glue and a few fiberglass strips. In this way, the magnet was suspended at about 3 cm from the top of the turtle's head and was free to make small random oscillations. These random movements ensured that unpredictable variations in the applied magnetic field were produced and thus prevented turtles from recalibrating their magnetic sense (see also [17]). Magnets used were of the same model as in a previous study [6], i.e., they were neodymium cylinders (type Neo 35, Calamit Trading, Milan) able to mask the geomagnetic field all around the turtle head (see [6] for a complete description of the magnetic fields produced). The black rectangle represents the magnet inside the epoxy resin.

(B) Homing routes of MT turtles (magenta) and of controls (black, releases 3–5). Different symbols refer to different turtles. The blue stars stand for the release sites, and the blue dot stands for the location of Saziley beach on Mayotte Island.

(C and D) Homing routes of MH turtles (red) and of controls (black) in releases 1 and 2 (C) and 3–5 (D). The routes of controls are shown in both panels (B) and (D) to facilitate comparisons with experimental turtles. Other explanations are as above.

northern part of the Mozambique Channel (see [Experimental Procedures](#) for details) and assessed their mechanical impact on the turtles' homing journeys. During the tracking periods, currents were quite variable in time and space and were mainly linked to the occurrence of local sea-level anomalies and associated eddies. The turtles' behavior in relation to these currents was variable too: in some cases, the turtles' movement was directed against the current flow, whereas in other instances the turtles tended to follow the currents (Figure 2 and Movie S1 in the [Supplemental Data](#) available online). This latter behavior was especially evident in the 2005 releases when some turtles moved in fair accordance with the substantial currents associated with a large anticyclonic eddy (Figure 2B) during long parts of their homing trips.

The quantitative estimation of surface current velocities allowed us to remove the current contribution to the recorded (ground-related) movement of each turtle

and thus to compute the water-related heading vectors, which represent the swimming movements actually made by the turtles in the various phases of their homing trip ([7], see inset in Figure 2B). The sequence of heading vectors obtained in this way for each turtle's ground-related path constitutes a corresponding water-related "motor path" (Figure S1). Mean current speeds along the tracks ranged between 12.6 and 32.2 cm/s, whereas turtles were found to swim 1.7–5.4 times faster than this (current contribution excluded). The movements recorded were therefore largely determined by the turtles' active swimming. Computer simulations of the movements of virtual turtles passively drifting within the same current field as the experimental individuals indicate that no drifting turtle could have reached Mayotte within one month after release [21].

We then evaluated turtles' ability to compensate for current drift by comparing the homeward components of the calculated track and heading vectors for single

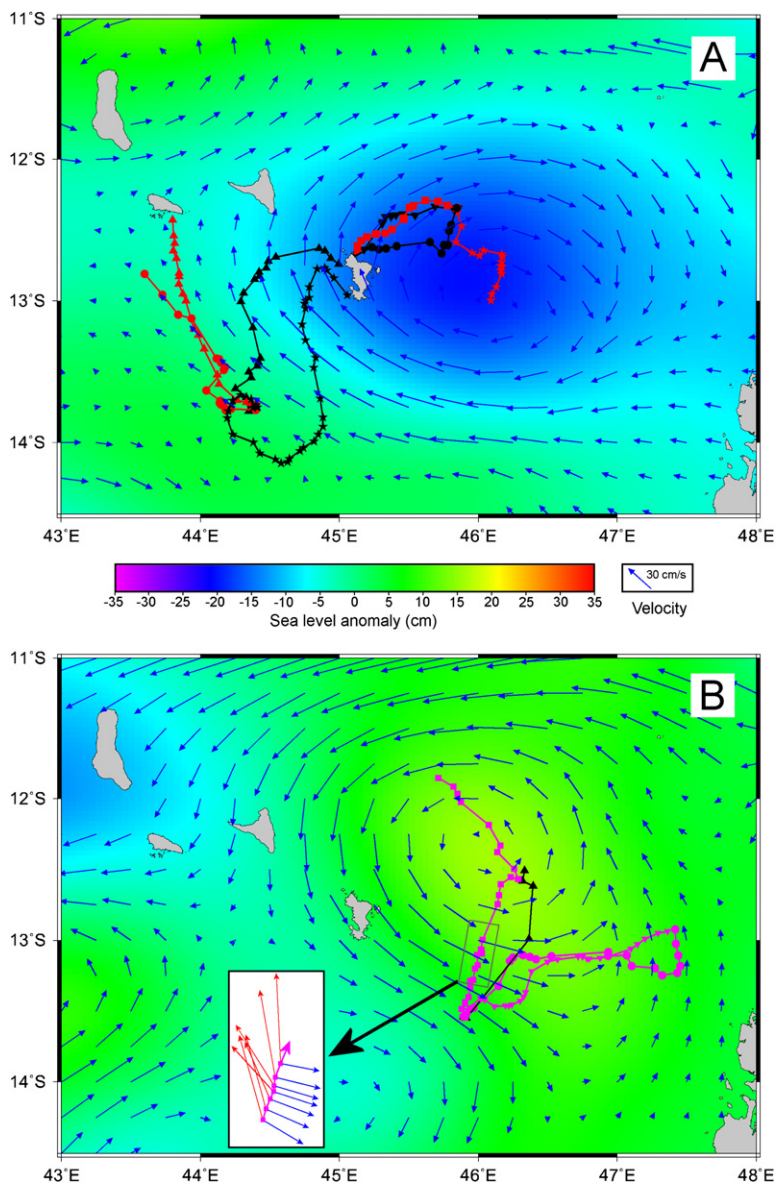


Figure 2. Examples of Turtle Movements in Relation to Ocean Currents

The initial parts (4 days) of the turtles' routes are plotted together with the surface current field estimated for the northern Mozambique Channel for the second day after release: (A) June 16, 2004 and (B) May 26, 2005. The current vectors (blue arrows) and the routes are superimposed on an image of sea-level anomalies for the corresponding day; these anomalies are representative of the eddies that were mainly responsible for the currents in the area at these times. The inset in (B) shows a 24 hr track segment of an MT turtle (on 26 May 2005) showing, for each interpolated location (every 4 hr), the estimated current vector (blue) and the deduced, water-related heading vector (red) representing the actual swimming movement made by the turtle at each 4 hr step. The scale of the inset is the same as that in the main panel. Other explanations are as in Figure 1. See also Movie S1.

turtles; if a turtle indeed compensated for drift, its motor path would have been less homeward oriented than its track path, with the opposite occurring in the absence of drift compensation. Such within-subject comparisons of homeward components (in subsampled datasets to allow for statistical independence; see [Experimental Procedures](#)) were performed on six of the seven control turtles (there was not enough data for the remaining one; this procedure was not applied to MT and MH turtles because magnet application may have prevented them from determining the home direction). They revealed that the mean homeward component of the track path was significantly lower than that of the corresponding motor path in all cases (Wilcoxon signed rank tests:  $p < 0.05$  or less). This result confirms the conclusion of our previous study on three green turtles [7]: Considered individually, none of them was able to compensate for the current drift. To further investigate this issue, we performed a supplemental interindividual analysis by

comparing the straightness indexes of each turtle's track and motor paths in the seven control turtles. These indexes turned out to be significantly higher for motor, water-related paths than for track, ground-related paths (Wilcoxon signed rank test,  $T^+ = 28$ ,  $p < 0.02$ ), confirming at the population level that the orientation efficiency of motor paths is higher than that of track paths.

Because motor paths better represent the turtles' intended movements than track paths, the three experimental groups were then compared on the basis of the straightness indexes of the single motor paths instead of those of the track paths previously used ([Table 1](#)). A one-way ANOVA revealed a highly significant ( $F = 7.02$ ;  $p = 0.006$ ) difference among the three groups, with control turtles performing significantly better ( $p < 0.05$ ; Tukey test) than both magnetically treated groups, whose performances did not differ significantly from each other. Furthermore, we considered that a statistical bias may have been introduced in our global analysis by

the fact that, for logistical reasons, MT turtles were all released at the same site. We therefore performed additional two-sample tests on motor-path indexes by considering MT and MH turtles separately. Mann-Whitney tests revealed a significant difference between C and MH turtles (when all releases were considered;  $U = 8.5$ ,  $p < 0.04$ ) and between MT turtles and the three controls released at the southeast site ( $U = 0$ ;  $p < 0.025$ ). Thus, these tests independently confirmed the outcome of the global analysis and showed that the effects previously highlighted were not due to a release-site bias.

Despite the small sample size, the experiment yielded statistically significant evidence for both track and motor straightness indexes and showed a worsening in the homing abilities of both experimental groups after the experimental displacement from their nesting beach. Magnetic treatment en route was as effective as magnet application prior to release; the homing performances of the MT turtles were not significantly different from those of the MH turtles.

According to these findings, magnetic cues play a role in sea-turtle homing. It is difficult to determine the actual magnetic-field alteration produced by the attached magnets (given that they were randomly oscillating), but it can be safely estimated that they produced a disturbance of at least  $200 \mu\text{T}$  around the whole turtle head [6], where all the putative magnetoreception sites (e.g., trigeminal nerve, eye, and pineal gland) are located [22, 23]. The treatment therefore prevented the turtles from correctly detecting the Earth's magnetic field (whose total intensity is about  $33 \mu\text{T}$  in the Mayotte area; Table S1), making reliance on both a magnetic compass and location sense impossible (see [24] for a detailed presentation of the navigational impairments produced by magnet application). Attachment of (less powerful) magnets was indeed effective in disturbing the orientation of hatchling loggerhead turtles in arena tests, a response that could have derived either from an effect on a compass or from an effect on a position-finding mechanism, or both ([25]; see also [26] for preliminary experiments on magnet-equipped adult turtles). At present, it is difficult to understand how geomagnetic information is implemented in the turtles' navigational system or to assess which magnetic parameters (especially intensity and/or inclination [3, 27]) are involved in these processes. Magnet attachment does not make it possible to produce specific magnetic-field alterations detected by the treated animal. Because the location and the functioning of the putative magnetoreceptor are still debated, the artificial field actually produced at that site cannot be predicted.

The most immediate way by which displaced turtles may exploit magnetic cues would be to rely on some kind of "magnetic map" [2, 3, 8, 28, 29]. For instance, newborn loggerhead turtles and juvenile green turtles have been shown to detect differences in magnetic-field intensity and inclination and to display appropriate orientation responses in arenas when they are presented with these two parameters in specific combinations that simulate long-distance translocations [4, 30]. At least for juvenile green turtles, these results have been interpreted as indications of reliance on navigational magnetic maps, possibly at a coarse resolution [3, 4]. In the Mozambique Channel area, magnetic-field conditions

are indeed quite favorable for reliance on such a magnetic map because inclination and intensity gradients are quite uniform and intersect each other at wide angles so that they form a grid potentially suitable for navigation (data from IGRF model, see also [29]). The behavior of the MH turtles is in accordance with such a mechanism; displaced turtles that use magnetic information would be greatly affected by magnet attachment at the release site in that they would be unable to properly evaluate the geomagnetic parameters after release and hence would be unable to establish their present location in relation to home. Our results, however, do not allow us to determine whether the effect recorded in the MH turtles is only due to a disturbance of their location-fixing mechanism because a similar impairment would have also been recorded if the MH turtles were relying on nonmagnetic positional information and on a magnetic compass to determine the home direction.

Conversely, the impairment shown by the MT turtles, which were treated only during transportation to the release site, is not directly explainable by an effect on a navigational mechanism based on geomagnetic cues detected during homing. These turtles were not wearing magnets during their homing trip, and so they should have been able to collect positional information while homing (at the latest after recovering from the treatment), whereas they were as disturbed as the MH turtles. This rather surprising finding indicates a possible navigational role of geomagnetic information collected during (passive) transportation; this information may have provided untreated turtles with some indications on the displacement direction [28]. For instance, displaced turtles might have sensed swell-induced accelerations of the boat and have consequently assessed, at least crudely, the general direction of travelling with respect to their magnetic compass. Such a reliance on navigational information collected during passive transportation is actually known for pigeons; in these birds the ability is based on olfactory cues [31], but a complementary role of compass magnetic information has also been proposed ([32], but see [33]). An alternative possibility is that magnetic disturbance during transportation may have persisted for some time after the removal of magnets, and this may have rendered the MT and MH turtles functionally equivalent during their homing journey. For instance, the magnets' field may have physically altered magnetite particles possibly involved in magnetoreception, with an effect lasting longer than magnet application. In this view, the application of strong magnets might have had an effect similar to that of pulse magnetization treatments, altering for some days orientation responses mediated by magnetite-based magnetoreceptors [22]. To our knowledge, long-lasting after-effects of magnet application have not been described, nor can they be immediately inferred from the proposed models of animal magnetoreception [23]. However, such a possibility cannot be dismissed.

A number of characteristics of the homing routes of the tracked turtles (controls included) remain unclear; these include the initial northward movements common to all the 2005 turtles and the tendency to follow indirect, curved routes to home (as already recorded in previous displacement experiments [15, 16]). These

characteristics are not readily explainable by current action alone (see above) and may indicate bicoordinate navigation based on nonorthogonal gradient fields [34]. A careful analysis of the relationship of the turtle water-related movements with the other environmental (and possibly navigational) factors present in the area would be helpful in this respect. Most likely, the homing turtles relied on additional, nonmagnetic navigational cues that may have contributed to shaping the turtles' routes, besides allowing the magnetically disturbed turtles to home (even if less efficiently than controls). It is currently hard to figure out how magnetically treated turtles managed to home. Following previous suggestions [15], one may hypothesize that Mayotte turtles homed thanks to a beaconing process [28] based on locally available navigational cues. For instance, homing in Ascension Island green turtles is known to be easier from the downwind side of the island, with wind-borne cues having been proposed to play a major role in the final homing steps [15, 16]. During our experiments, winds around Mayotte were mostly blowing from southern quadrants (information provided by local measurements and Quikscat satellite wind observations), which might have favored the prevalence of island approaches from northern directions (Figure 1). Ocean currents, conversely, do not seem to bear useful navigational information for displaced turtles [7, 15].

In conclusion, the present experiment provides the first field-collected evidence of the involvement of geomagnetic cues in the navigation of freely moving sea turtles and suggests a so-far-unsuspected navigational role of magnetic information collected during passive transportation to the release site. It is currently difficult to provide a full and detailed interpretation of the present findings. However, because the magnetically disturbed turtles did home, our findings show that the geomagnetic field provides important, although not essential, cues for sea-turtle navigation after displacement. These conclusions are in accordance with similar indications obtained through arena experiments in juvenile turtles [4] but are somewhat at variance with those deriving from a previous field experiment showing that magnet attachment did not affect the navigational performances of Ascension Island green turtles during their oceanic migration toward foraging sites along the Brazilian coast [6]. However, because nonmagnetic cues are likely to be involved in sea turtles' homing processes (as also indicated by the present experiment), it may be hypothesized that although nonmagnetic cues alone may be sufficient to allow efficient open-sea navigation directed to large goals (like the Brazilian coast), geomagnetic information has a major, albeit still not exclusive, role in pinpointing isolated targets.

#### Experimental Procedures

##### Displacements and Releases

The experiments were carried out in May–June 2004 (releases 1 and 2) and 2005 (releases 3–5), i.e., just before the peak of the green turtle nesting season in Mayotte. Environmental conditions with regard to water temperature, wind patterns, and meteorology were broadly similar in the two experimental periods (this information was provided by the local meteorological station and by satellite-derived data on sea-surface temperatures and wind stress). Thirteen of the 20 turtles were captured before they laid their eggs; the remaining

ones were captured after nesting was completed. Individuals of these two categories were equally distributed in the various treatments. After capture at night, turtles were kept confined singly in wooden crates on Saziley beach. On the following day, Argos-linked satellite transmitters were glued to the turtles' carapace by means of fiberglass stripes or epoxy resin, and the cable ties used for magnet attachments were glued to the central scute of the turtles' head (Figure 1A). Control turtles had brass disks identical in size and shape to the magnets, and these were attached to the head in the same way without, however, producing any magnetic disturbance. The transmitter models used—Telonics A-210, A-410, and A-1010—have all been previously applied to adult turtles with success [6, 7, 15, 16]. Models A-210 and A-410 only slightly differ for their size and weight (maximum dimension 10.2 to 13.0 cm; weight 190 to 215 g; see [www.telonics.com](http://www.telonics.com)), whereas the somewhat bigger A-1010 has been applied only to control turtle C1. The different models employed are therefore unlikely to have differentially affected the behavior of large (>120 cm long) adult turtles. Having been attached on the first central scute of the carapace, i.e., around 40 cm from the head, the transmitters produced negligible magnetic disturbances at the brain level (see [6, 24] for more information on this aspect).

The turtles were then loaded onto a 12 m wooden sailboat powered by an outboard motor. They mainly stayed aligned with the head facing the prow. During transportation, turtles were mostly prevented from accessing visual navigational cues; the sea view was screened by the crate's and the ship's sides, and sky cues were screened from above by moist cloths and screens that were placed on the turtles' head and/or above the crates to keep them cool. Moreover, in releases 1, 3, and 4, the journeys were performed at night and/or under overcast conditions. Once at the release site (trip durations around 12 hr), the turtles were set free by removing the wooden crates and lifted overboard or induced to move toward the bulwark-free back side of the boat from where they could freely slide into the sea. Each turtle was released singly, a few minutes after the preceding one.

The release sites were chosen as to be symmetrically distributed around Mayotte and far from the other Comoros islands. They were located outside the usual migratory pathway of the Mayotte-nesting green turtles, which migrate westward to feeding grounds along the Mozambique/Tanzanian coast (D.R., unpublished data). All releases were planned at 120 km from Saziley beach, but releases 2 and 3 had to be made at 100 km because of the presence of a sand mount at 120 km or bad weather conditions, respectively. Magnetic parameters at the release sites differed by 0.14–0.22  $\mu$ T in intensity and by 0.6°–1.3° in inclination with respect to Saziley beach (see Table S1). Of the 18 turtles that returned to Saziley, nine were observed on the beach again. Two of these were MT turtles. Among the remaining ones, one MH turtle, and two controls still had the magnet or the brass disk attached on the head, whereas two controls and two MH turtles were found with only the glue but without the cable ties and the disks. It is likely that these turtles lost their magnet or disk while staying in the coral reef around Mayotte (e.g., in cavities where they are known to rest before emerging for egg laying). In any case, even if the loss of the magnet in MH turtles had occurred during the homing journey, this would have minimized the difference between MH and C turtles, making the detection of a significant difference less likely.

##### Route Reconstructions

Tracked turtles were localized by the Argos System, which classifies the locations into six classes of different accuracy levels (see [www.argosinc.com](http://www.argosinc.com)). We reconstructed the routes by using sea locations (i.e., discarding land locations) and filtering out low-accuracy locations as follows. For each individual, we first determined a speed threshold from high-accuracy locations and then discarded all the locations resulting in speeds above that threshold. In addition, we removed locations involving changes of direction larger than 120°. The turtles were considered to have successfully homed as soon as they were located inside or close to (<5 km) the lagoon surrounding Mayotte, where the homing mechanism used may be different from that employed in the open sea.

##### Estimation of Ocean Currents

Because green turtles' oceanic movements take place in the upper layers of the water column (10–20 m depth [35]), the currents

experienced by turtles were estimated with satellite-derived oceanographic data according to the procedure described in [7]. In short, surface velocity fields were computed on a daily basis as the combination of (1) geostrophic current anomalies, derived from the DUACS gridded altimetric sea level anomaly product (Topex/Poseidon and ERS satellite data; see [www.jason.oceanobs.com](http://www.jason.oceanobs.com)); (2) mean geostrophic surface currents, calculated from the mean dynamic topography [36]; and (3) Ekman (i.e., wind-induced) currents, derived from Quikscat scatterometry (see [www.ifremer.fr/cersat](http://www.ifremer.fr/cersat)).

#### Path Analysis

The filtered turtle locations were first standardized as a fix every 4 hr by linear time interpolation. The current data similarly underwent a bilinear spatial interpolation and a time linear interpolation so that the current vectors corresponding to the turtles' locations every 4 hr could be estimated. At each of these locations, we then computed the water-related heading vector of the turtle by subtracting the current vector from the ground-related track vector (see [7] for details). In this way, for each of the twenty turtles, data were summarized in the form of a (ground-related) track and a (water-related) motor homing path.

The orientation efficiency of track and motor paths was estimated with the generalized straightness index  $(D_i - D_f)/L$ , where  $D_i$  is the initial homing distance (between the release site and Saziley),  $D_f$  is the final homing distance (between the last path location and Saziley), and  $L$  is the distance travelled. This index (which obviously reduces to the classical straightness index  $D_f/L$  when the animal reaches its home at the end of its path) has been shown to constitute the most reliable measure of the efficiency of an oriented path because it corresponds to the mean cosine of directional errors computed at a high spatial frequency [19]. The computation of this index for track paths is straightforward. For motor paths, a more complex approach is required because these paths cannot be suitably represented in a geographical (earth-bound) system of reference. The motor straightness index thus has to be computed either on an ad-hoc path representation where the home is virtually located at infinity (Figure S1; see also [7]) or as the mean cosine of the motor directional errors, i.e., of the discrepancies between the turtle headings and the home direction measured at a high spatial frequency (every 1 km in the present case). Both methods are strictly equivalent and obviously provide fully consistent results if applied to track paths. Parts of the motor paths within 20 km of a coast or a reef barrier were not taken into account in this computation because the ocean current estimates are known to be unreliable in this context.

We performed within-subject analyses to assess the turtles' ability to compensate for current drift by computing the homeward components of heading and track vectors as the cosines of the angular differences between the home and vector directions. This was done for every interpolated open-sea location (>20 km from coast or reef) where the current speed was above 25 cm/s. To avoid serial autocorrelation, we subsampled these location data by taking only one every  $n$  locations, where  $n$  is the minimum integer value specific to each path, allowing for statistical independence (at  $p > 0.1$  based on an angular rank correlation test) for both heading and track vectors (see [7]). The mean track and motor homeward components were then compared with Wilcoxon signed rank tests.

#### Supplemental Data

Supplemental Data include two movies, one table, and one figure and are available online at <http://www.current-biology.com/cgi/content/full/17/2/126/DC1/>.

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