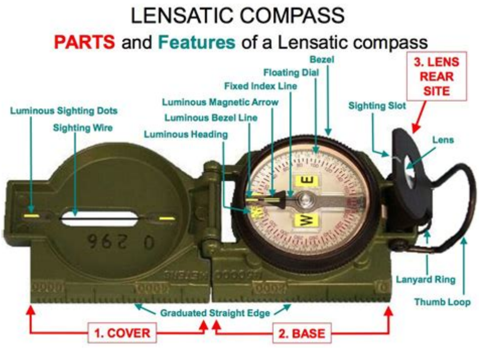

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Like a Compass, it can and should be used anywhere in Europe by anybody interested in human rights, democracy or citizenship. This is our global evidencebase for youth policy.Sign up for our lowvolume newsletter below. Prefer visuals We are on Flickr and Vimeo. Fancy a chat Ping us on Twitter or Facebook wed love to hear from you. Most other places would Itll make you feel better, wont it. If you use Pay Pal, use the link below. Use the above address for a check, M.O. or cash. We distinguish between the known use of the suns azimuth to provide absolute geographical direction compass mechanism and its possible use to detect changes in heading heading indicator mechanism. Just as in an aircraft, these two kinds of information may be provided by separate mechanisms and used for different functions, for example for navigation versus steering. We also argue that although a solar compass must be timereferenced to account for the suns apparent diurnal movement, this need not entail full time compensation. This is because animals might also use timedependent solar information in an associatively acquired, and hence timelimited, way. Furthermore, we show that a solar heading indicator, when used on a sufficiently short timescale, need not require time compensation at all. Finally, we suggest that solarderived cues, such as shadows, could also be involved in navigation in ways that depend explicitly upon position, and are therefore not strictly compassrelated. This could include giving directionality to landmarks, or acting as timedependent landmarks involved in place recognition. We conclude that clock shift experiments alone are neither necessary nor sufficient to identify the occurrence of all conceivable uses of solar information in animal orientation, so that a predictable response to clock shift should not be regarded as an acid test of the use of solar information in navigation.http://www.mogadicho.com.br/6es7-314-1ae04-0ab0-manual.xml

a The sun itself can serve as a timedependent landmark in conjunction with the landscape, as in this painting of an avenue of poplars at sunset by Van Gogh Nuenen, October sunset, 1884, in which we assume that the woman is walking towards the viewer. Each trajectory covers an entire 24h period for the insight that this yields; that period during which the sun would not be visible is shown by a dashed line; the filled circles mark hourly intervals. To read the graphs, simply pick a release time in GMT and follow the trajectory forward in time from this point. Download fulltext PDF We disti nguish between the known use of the suns azimuth to provide absolute geographical direction compass mechanism and its possible use to detect changes in heading heading indicator mechanism. Just as in an aircraft, these two kinds of infor mation may be provided by separate mechanisms and used for different functions, for example for navigation versus steering. We also argue that although a solar compa ss must be tim e referenced to account for the su ns apparent diurna l movement, this need not entail full time compensation. This is because animals might also use timedepen dent solar information in an asso ciatively acquired, and hence timelimi ted, way. Furthermore, we show that a solar heading indicator, when used on a suf.Finally, we suggest that solarderiv ed cues, such as shadows, could also be involved in navigation in ways that depend explicitly upon position, and are therefore not strictly compassrelated. This could include giving directionality to landmarks, or acting as timedependent landmarks involv ed in place recognition. W e conclude that clock shift experiments alone are neith er necessary nor suf. Published on behalf of The Association for the S tudy of Animal Behaviour by Elsevier Ltd. Although not the only compass that birds use, the sun compass appears to be dominant in diurnal species.

As a very distant but highly visible object, the sun can provide reliable compass guid ance because its geographical direction effectively does not change as the animals position changes. However, the Earths spin pro duces an arc of apparent movement of the sun across the sky through the day, and this means that the suns geographical di rection does change slowly through time. R emarkably, birds appear capable of learning enough about the pattern of the suns directional movement through the day to compensate for it, and hence to use the sun as a compass. Published on behalf of The Association for the Study of Animal Behaviour by Elsevier Ltd. This is an open access article under the CC BY NC ND license . Animal Behaviour 97 201 4 135 e 14 3 Fundamentally, this is an ideas paper in which we revisit the sun compass concept and suggest that while birds almost certainly do use a timecompensated sun compass in the classical sense, this does not e xclude the possibility that they use solar cues in other way s for orientation. Some other uses of solar cues have been proposed previously. For example, it was once conjectured that the sun might provide birds, and other longdistance migrants and navigators, with po sitional information on a global scale, and not just with directional information. Mathews sun arc hypothesis Baker, 1 978 recognized that latitudinal information from the suns arc, and longitudinal information from the time of dawn, dusk or zenith, when compared with the time of these events at home, could provide an animal with an approximate position on the Earths surface, a fact long exploit ed by mariners in possession of ephemeris data, a sextant and a chronometer. But the experimental data largely did not.For this reason, we do not consider Mathews hypothesis further here.

Instead, we put forward a number of different way s in which solar cues may provide direc tional information on a more local scale, and articulate a number of problems with current acceptance of the mainstream hypothesis. In particular, we distinguish between varying degrees of time compensation, suggesting that the sun can be a useful compass even if it is not fully timecompensated but instead is used in more restricted, timelimited way s. We also argue that solar cues may be used for certain functions in orientation without the need for time compensation at all, such as in maintaining a course that has already been set. Finally, we argue that solar cues may provide guidance by modifying the appearance of the landscape, whether by giving direction to landmarks through shadowing, or by adding distinctive components to the visual appearance of a place that become salient during learning and recognition. WHA T A COMP ASS IS W e recognize that in introducing mechanistic distinctions that may previously have been overlooked, there is an inherent danger of semantic confusion. This distinction is not as obvious as it sounds. For example, in the cockpit of most aircraft there is, in addition to a magnetic compass, another instrument called a heading indicator. This looks very much like a compass, being marked with the cardinal directions and a 360 scale. However, the heading indicator is just a gyroscope that holds its direction in an inertial frame of reference, which for practical purposes means holding direction with respect to the stars. A heading indicator can therefore only provide absolute geographical direction with respect to the Earths surface if its direction is calibrated against some ext ernal reference such as a magnetic compass or the known direction of a runw ay. Even then, it needs to be recalibrated peri odically to compensate for the steady drift that results from the Earths spin.

Nevertheless, the heading indicator serves a crucial purpose in allowing the pilot to steer a course while making turns whose acceleration would cause a magnetic compass needle to deviate from north. As we discuss below, the sun and its attendant cues could serve as a heading indicator in birds, with no require ment for time compensation when used to steer over suf.The distinction between a solar compass and a solar heading indicator is an important one, therefore, which the animal navigation literature has previously ignored. THE SUN AS A COMP ASS A compass is a mechanism that indicates absolute direction with respect to the Earths surface, wherev er it is placed. A direction may be said to be absolute if it is known relative to some geographically. For example, a magnetic compass indicates absolute direction relative to the local magnetic.A solar compass, on the other hand, indicates absolute direction relative to the local meridian running north to south between the poles of the Earths spin. T o inform an animal of this direction, however, a solar compass must somehow be compensated for the apparent mo ve ment of the sun across the sky as the Earth spins. Because this movement is regular and predictable, such compensation can of course be achieved by reference to an accurate internal clock. This is not the only possible compensation method, however, especially if solar information is being used in a timelimited way. North of the Tropi c of Cancer, for example, the sun always lies south when it reaches its zenith, so on any given day of the year, the shortest shadow that an object casts alway s points north. Likewise, at lati tudes close to the equator, a line drawn between the tips of the shadows cast a few minutes apart by the same object alway s points appro ximately to the west.

We do not necessarily mean to say that birds make use of these heuristics, or of the man y others that can be derived from them; rather we mean to show that full time compensation is not the only way to derive true compass infor mation from the sun. Degrees of Time Compensation Classically, because the suns azimuth changes through the day, the sun compass has been regarded as req uiring time compensa tion. However, this leav es open the question of the accuracy or degree to which time compensation occurs.So, if return home from a particular direction alway s occurred at roughly the same time in the evening, say, then the sun might be used to provide just a single direction, limiting its effectiveness to that particular time of day. A more varied experience of return directions might allow the animal to learn that the evening suns direction could be used as a more general reference, still in a timelimited way, but with different homing tasks req uiring different.Full time compensation would provide a more general compass still, but an additional degree of informational complexity is needed to achieve this g enerality not only is the appropriate.The value of full time compensation is that birds are able to generalize across instances of directional guidance informed by the suns position at different times of day, and to use this generaliza tion to extrapolate to unusual that is, not yet experienced times of day. It is therefor e a distinctly cognitive concept, allowing.With suf cient generality across experiences of time, we might even say that the animal had dev eloped full time compensation. Howev er, the extents to which animals have a dedicated template for linking endogenous time with the suns direction, form truly cognitive constructs of time compensation or, more simply, gener alize to their closest temporal experiences are unanswered questions. Evi dence is equiv ocal. On the other, Budzynski et al.

200 0 showed that pigeons can learn to use the suns direction to locate a food goal in an arena at least appro xi mately at an unfamiliar time of day in the morning whether they hav e experienced the suns movement during the entire day controls or only during the afternoon experimental birds. These results accord with.Nevertheless, at least one pigeon in Budzynski et al.s 20 00 experiment apparently learnt to use the sun as a.How could different degrees of time compensation be distin guished. SchmidtKoenig 1 958 w as the.The idea is that since the bird chooses a.The result is very general, but pigeons in particular reliably show full clock shift ef fects when displaced to release sites that can con.However, an effect of clock shif t does not necessarily distinguish full time compensa tion from a simpler, more limited use of time compensation. An animal using more limited time compensation might also respond to clock shift with deviated orientation if released at an unusual, and biased, time of the natural day as a consequence of the experimental procedure. So, strictly, demonstration of full time compensation req uires demonstration that deviation in orientation under clock shift is not dependent on the time of day at which the birds are trained and released. T o elaborate, if an animal alway s experiences the suns position to be in appro ximately the same direction following a repeated experimental or natural displacement, then it could learn that this direction can be used t o provide guidance on the return journey. Subsequentl y, displacement at a time of day when the sun in fact had a different azimuth might then lead to shifted orientation, precisely because the bird was not employing time compensation for the suns movement.

Following experimental clock shift, the av ailable release window in which both actual and subjective daytime coincides is shortened, towards the end of the natural day for slow shifts or the start of the natural day for fast shift s, poten tially inducing deviation biases in the same directions as those predicted by time compensation if experimentall y shifted birds are consistently released later slow or earlier fast during testing than during training. One test for this limited form of time compensated compass would be to investigate the orientation of unshifted birds at the same biased time of day, for they too should be similarly affected. This should of course happen normally in wellconducted experiments in which experimental releases are temporally interleaved with controls. Our point here is not that full time compensation is unimportant, unreal or undemonstrated, but rather that birds may also make use of the sun in a simpler, more limited manner that could in.The point we wish to make then is that a true sun compass need not be fully timecompensated to be useful, and that deviation under clock shift is not necessarily suf.This is because time compensation could take man y forms, some poten tially very restricted in their use, and it could emerge simply, but idiosyncratically, as a result of the animals particular prior expe riences. This idiosyncrasy might even explain some of the high variability that emerges in the results of clock shift experiments see e.g. Chappell, 1 997 , although of course other accounts are possible, for example to do with the poorly understood processes of rephasing the internal clock. THE SUN AS A HEADING INDICATOR Having set a heading by whatever means, animals, like aviators, must make continued use of directional information in order to maintain that heading.

Although it is possible in principle to use a compass for this task, the directional information that is required to maintain a heading need not involv e an y absolute geographical reference at all. The value of this simpler kind of directional infor mation will be familiar to an yone who has strayed from a footpath in dense forest,.Surfacebound animals may use idiothetic cues associated with w alking on a substrate to achiev e this, but such cues are absent when moving through the air. On the other hand, the sun and its attendant cues, such as the polarization axis of the sky, provide a reliable celestial heading reference, analogous to the inertial heading reference provided by the gyro scope in an aircrafts heading indicator see abov e. Indeed, before the advent of GPS, pilots.Likewise, sun compasses were routinely used by the British Army to set and maintain heading in the featureless deserts of North Africa and the Middle East during the Second W orld W ar and First Gulf W ar. As a rule of thumb, the sun com passes used in these con.This is because heading at a constant angle to the sun produces only a slight curvature in tra jectory, and the deviation from a straight path is scarcely noticeable on so short a timescale.Clearly, the curvature of so wide an arc would be indiscernible over a few minutes of. In particular, because the offset correction would be made on the basis of time elapsed, rather than time of day, it would not be susceptible to perturbation under clock shift.Once again, the curvature of these tra jectories is indiscernible over a few minutes of. Once again, because the offset correction would be made on the basis of time elapsed, rather than time of day, it would not be susceptible to perturbation under clock shift. It is important to emphasize that neither the uncorrected solar heading indicator mechanism Fig. 1 a e c nor the offsetcorrected solar heading indicator mechanism Fig. 1 d e f meets our de.

Rather, each hypo thesized mechanism simply allows an arbitrary heading to be maintained with a reasonable degree of accuracy on timescales of a few minutes to a few hours, dependent upon whether or not an offset correction is applied. Nevertheless, the simpler kind of directional information that this mechanism provides could still be of immense value to an animal in maintaining, and indeed reversing, a course. W e discuss these possible functions of a solar heading indicator further below. POTENTIAL FUNCTIONS OF DIRECTION AL SOLAR INFORMA TION A Compass for Navigation The.It has long been recognized that the sun can provide the necessary compass information in this second step. But to these two steps we should perhaps add a third, in which directional information is used to maintain a heading that has been set, without updating that course on the basis of some updated estimate of position relative to home. This third step is important, because it allows the animal to make progress towar ds a goal without having to reassess its position constantly. Indeed, it might also allow the trav ersing of areas in which na vigational information is for some reason unavailable or highly confused, freeing the bird from potential navigational traps. Adding or distinguishing this third step may seem an unnec essary complication, but is important in making clear our key point that different solar information might, in principle, be used for different aspects of mapandcompass navigation. This could have important consequences for our interpretation of the results of clock shift experiments. For example, the nding that a clock shifted bird tends to.Neither interpretation ex cludes the possibility that a bird still makes use of the sun as a heading indicator to assist in holding course once an initial heading has been set.

Like the mapandcompass model, the mosaic map also uses compass information to inform a trav erse betw een known focal places, with the advantage that the animal does not need to know where it is all of the time, allowing a more ef.Hence, just as in mapandcompass navigation, solar information could usefully serve as a heading indicator on the short timescales involved in tra versing between focal places when using a mosaic map. In summary, although the mapandcompass and mosaic map concepts both de.Illustration of the principle of a solar heading indicator, showing the trajectories that would be followed by a, b, c a bird that always.Each trajectory covers an entire 24 h period for the insight that this yields; that period during which the sun would not be visible is shown by a dashed line; the.T o read the graphs, simply pick a release time in GMT and follow the trajectory forward in time from this point.The simpler directional information provided by a heading indicator is suf.It follows that both timereferenced and nontimereferenced solar information could in principle be involv ed in both kinds of homing process. A Compass for Racing A compass may also be used to home over long distances in a simpler way than envisaged by either true navigation or the mosaic map. With repeated training from just a single direction, birds hav e the opportunity to learn that their goal can alway s be reached by attending to compass information alone. Indeed, it is common practice in the sport of pigeon racing to train birds to. An associative account might be that a single compass bearing always provides reliable guidance for homing, so that racing birds learn to ignore other navigational cues, at least until they are near home, thereby enhancing their performance, especially in very long races.

A solar compass used for this purpose would need to be well time compensated to be effectiv e, but it would not need to involv e any conte xt of position, and certainly no map, because the goalw ard direction is invariant. It is not obvious that a racing compass would have much natural use, for it would rely on resources alway s being located in the same direction, but it seems analogous, at least, to the innate compass orientation of.We should ther efore be wary of it in scienti.Some experiments demonstrating an effect of clock shift af ter extended training from a single familiar site may, in fact, have stumbled upon this kind of compass use. Entrained directional orientation can dominate initial orientation after rather few releases as few as three in Michener and Walco tts 1 967 studies, so we must be cautious of generalizing about compass function from such situations. Directional Information for Steering Time compensation is only strictly necessary if the sun is to be used to locate a particular geographical direction at an arbitrary time of day. If direction is req uired only for steering a straight course, or for measuring drift aw ay from it, then the suns azimuth could be used without true time compensation. In this case, we would regard the sun as a heading indicator. Of course, there is no reason why timecompensated solar information should not be used for steering also, and in this case we would regard the sun as a compass. The distinction that we are drawing here is not merely a semantic one, because the directional information that a solar heading indicator provides is expected to be invariant under clock shift, in contrast to the directional information provided by a time compensated sun compass see above. W e suggest three related scenarios in which birds might use directional solar information for steering. First, a ying animal might use the sun to maintain a constant heading towards a target with which it is not in sensory contact.

W e have mentioned this already in relation to the use of the sun as a heading indicator in the mapandcompass and mosaic map models of navigation. However, the same mechanism might also fare in explor ation, where there is no speci.Second, a ying animal might use the sun for steering when it needs to measure changes in heading angle made in the course of exploration, or in avoiding obstacles. Thus, timeindependent use of the sun as a heading in dicator could be a common mechanism in the path integration systems used by many animals to compute and update their current direction to home when their outbound track is not straight. Third, a ying animal might use the sun for steering even when it is in direct sensory contact with the visual landmarks that it is using for guidance. This point requires a little further explanation, but as we now show, the most obvious bene.If a bird heads directly for a distant, visible landmark, then a crosswind will lengthen its geographical path and produce a curved geographical tra jectory. The same phenomenon occurs on, or in, moving wate r. Windward drift can be avoided by adjusting heading into the wind, which is precisely what an air crafts pilot does when making a crabbed landing on a runw ay with a strong crosswind, but it requires recognition of the drift aw ay from a straight track. Although it is possible to detect wind drift by attending to the relative motion of the underl ying landscape, a more reliable method is simply to adjust the heading so that the target remains on a constant bearing. Adjusting the heading so that the angle between the target and the sun is kept constant will produce a geographically straight tra jectory to the target over pe riods of time short enough that the suns own geographical direc tion does not change signi cantly.

OTHER POTENTIAL USES OF SOLAR INFORMA TION W e have focused so far upon categories of directional solar in formation that use the sun either as a compass or as a heading indicator. However, the po tential roles of solar cues in navigation and orientation may be richer and more complex still. First, we consider how the timedependent effects of the sun can change the visual appearance of landmarks, and suggest that in extreme cases this could lead to a failure to recognize a place when viewed at an unfamiliar or incorrectly interpret ed time. Second, we consider how the timedependent effects of the sun can visually superim pose directionality on landmarks in the visual scene. Timecompensated Landmarks W e are used to thinking of the sun as providing compass in formation because its geographical direction remains essentially.Compare the two representations of the same visual scene painted at different times of day in Fig. 2 b and c. For visual cues to be used to recognize a place as a single familiar location at any time of day, this timedependent information must somehow be parsed out of the common representation of the place. It is possible, of course, that animals only memorize those fea tures of the visual landscape, such as the relief of the horizon, that do not vary with the suns position. This would happen automati cally under the simplest associative account of visual scene recognition, provided that the scene were viewed at different times of day during learning. This is because the features of the scene that the animal learns to associate will be those that are the most reli able across occasions. But if the animal is alway s trained to learn the same scene at the same time of day, then its learned representation of the scene will be intrinsically timelimited.