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Right hemisphere advantage in the development of route fidelity in homing pigeons

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Several laboratory studies have revealed functional hemispheric lateralization in birds performing visual tasks. However, the role of functional brain asymmetries in spatial behaviour in natural settings is still poorly investigated. We studied monocularly occluded homing pigeons, *Columba livia*, to investigate potential differences in the hemispheric control of navigational performance. We GPS-tracked monocularly occluded and control binocular homing pigeons during seven group training releases and a final solitary release from each of two sites. The pigeons were then given one last release from each site after a phase shift of the light-dark cycle under binocular conditions, to distinguish compass-based orientation from landmark-based pilotage. Overall, pigeons homing with the left eye/right hemisphere (RH) displayed a greater fidelity to the familiar space previously experienced than pigeons homing with the right eye/left hemisphere (LH). Another difference between the two monocular groups is that LH pigeons were more likely than RH pigeons to fly with other pigeons during the group training releases. The data support the hypothesis that the left eye/right hemisphere plays a more substantial role as pigeons develop fidelity to certain routes to home from familiar release sites, an enhanced fidelity that may be supported by superior memory for familiar landmarks.

Anatomical and functional hemispheric asymmetries are a ubiquitous property of vertebrate brains (Ocklenburg & Güntürkün, 2012; Vallortigara & Rogers, 2005). Because of their strongly lateralized visual systems (Manns & Ströckens, 2014), research on birds has made a substantial contribution to our understanding of the evolution, function and neural basis of the lateralized control of visually guided behaviour. Although the pattern of asymmetry may vary in the two most commonly studied avian species, young chickens, *Gallus gallus domesticus*, and pigeons, *Columba livia*, there is evidence that the two brain hemispheres of all birds asymmetrically support visually guided spatial behaviour (Nardi & Bingman, 2007; Tommasi & Vallortigara, 2001).

Pigeon homing is supported by a range of navigation and orientation mechanisms including the so-called navigational map, used from unfamiliar locations, familiar landscape/landmark navigation, sun compass and geomagnetic compass (Wallraff, 2005). There is considerable evidence that the two brain hemispheres make different contributions to supporting navigational mechanisms in pigeons. Navigation from unfamiliar sites, necessarily involving the navigational map and associated compass mechanisms, is principally controlled by the left brain hemisphere with respect to visual inputs (Prior, Wiltschko, Stapput, Güntürkün, & Wiltschko, 2004), hippocampal control (Gagliardo et al., 2001; Gagliardo, Vallortigara, Nardi, & Bingman, 2005) and control by the olfactory cortex (Gagliardo, Odetti, Ioalè, Pecchia, & Vallortigara, 2005). The left hippocampal bias correlates with the recently discovered broader neural network organization of the left hippocampus compared to the right (Jonckers, Güntürkün, De Groof, Van der Linden, & Bingman, 2015). By contrast, navigation by familiar landscape/landmarks appears more complicated and probably involves visual processing in both brain hemispheres (Diekamp et al., 2002) as well as both the left and right hippocampus (Gagliardo et al., 2002). However, interpretation of the familiar landscape/landmark lateralization data is confounded by the existence of two navigational strategies that can exploit topographical information in the control of homing behaviour: site-specific compass orientation and pilotage (Filannino, Armstrong,

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Guilford, & Gagliardo, 2014; Guilford & Biro, 2014; Gagliardo, Ioalè, & Bingman, 1999). Using the first strategy, birds rely on memorized release site features learned in association with the homeward compass direction. By contrast, relying on the spatial relationship among familiar visual features would enable pigeons to pilot home without being dependent on compass information, as such, resembling more the 'cognitive map' conceptualized by O'Keefe and Nadel (1978). These two strategies can be experimentally dissociated by releasing pigeons within a familiar area after having manipulated their internal clock, which induces a deflection in orientation only when the sun compass is being used because of an error in the estimation of time of day. The relative importance of familiar topographical cues for the reorientation of a pigeon can be evaluated by comparing the degree of deflection and/or the degree of overlap between tracks recorded before and after clock shift. Researchers using this protocol on pigeons housed in coastal Tuscany have discussed the important influence of the sea as a major guiding feature in enabling reorientation after clock shift (Bonadonna, Holland, Dall'Antonia, Guilford, & Benvenuti, 2000; Filannino et al., 2014; Gagliardo, Odetti & Ioalè, 2005). In fact, clock-shifted pigeons released from familiar locations outside visual contact with the coast consistently display a greater deviation from the home direction than pigeons released near the coastline, and this is true regardless of whether the phase shift-induced deflection led the birds to orient towards the sea or inland. Interestingly, hippocampal ablation impairs the ability to reorient at familiar locations where the coast can be used as a topographical cue (Gagliardo, Ioalè, Savini, Dell'Omo, & Bingman, 2009).

The possible differential involvement of left and right hemispheres for the visual processing of familiar landmarks for homing pigeon navigation remains uncertain, partly because, until recently, all experiments relied on vanishing bearing and homing speed data. In the current study, we applied GPS-tracking technology to record the entire flight tracks of the experimental birds to assess possible asymmetries in the contribution of left and right hemispheres in the visual processing supporting navigation by familiar landmarks or landscape features. Pigeons were first trained under monocular conditions (only the left or right eye had access to landmark/landscape information) from two training sites located near the coast north and south of home, and then tested under binocular conditions from the same sites, but now after a phase shift manipulation of the light-dark cycle. The phase shift manipulation was implemented to make the birds fly off initially in a wrong direction (induced navigational error; Wallraff, 2005). Using this two-step protocol, we could study the development of flight path fidelity under monocular viewing, and whether the left or the right eye visual system is advantaged in the learning of familiar topographical features during training that would enable a better landmark-based retracing of the acquired training route home after clock shift. We expected to observe a higher level of route fidelity during training and/or after clock shift in the pigeons trained with the hemisphere preferentially used for memorizing and recalling visual landmarks and landscape features associated with route fidelity. Alternatively, in the absence of any brain asymmetry in landmark-based route fidelity, one would expect better reorientation in the monocular group that had access to visual information from the coastline.

METHODS

General Procedure

We used 64 first-year, naïve pigeons of both sexes, hatched and kept at the Arnino field station (43°39′26″N, 10°18′14″E; Pisa, Italy). After fledging the birds were allowed to perform spontaneous flights around the loft. All releases took place under sunny conditions, with no or light winds over two summers (2013 and 2014). The birds had access to food, grit and water ad libitum for the duration of the experiment. The project was approved by the Scientific Ethics Committee of the University of Pisa (permit N. 24300) and was carried out in accordance with the EU Directive 2010/63/EU on the protection of animals used for scientific purposes. Two weeks before the experiment, the birds were equipped with PVC dummies to accustom them to carrying a load. A dummy was dorsally attached to a pigeon by means of a Velcro strip glued to the feathers, previously trimmed. During the experimental releases, the dummy was replaced with a GPS data logger (Mobile Action I-gotU, http://www.i-gotu.com/; 20 g), which stored every second latitude, longitude, speed and time of recording. The tracks recorded were visualized with QGIS (http://www.qgis.org/). The data used in this study are available on Movebank (movebank.org), study name 'Right hemisphere advantage in route fidelity in homing pigeons' (Data from Pollonara et al., 2017) and are published in the Movebank Data Repository with DOI 10.5441/001/1.245kb7r6.

Pigeons were randomly assigned to three groups. LH ($N = 23$) birds were trained with the left eye covered with an eye cap (see below). Therefore, because of the strongly lateralized, contralateral visual inputs to the telencephalon, these birds were prevailingly limited to left hemisphere visual processing. RH ($N = 25$) birds were trained with the right eye covered, and, therefore, right hemisphere visual processing. C ($N = 16$) birds were trained with both eyes uncovered. The three groups of birds underwent the following release programme from each of the two release sites chosen for the experiment (see below): seven group training releases; one individual release under nonclock-shifted conditions; one individual release following clock shift. Both LH and RH birds wore the eye cap during the seven group releases and the individual release under nonclock-shifted conditions, but were released in the binocular condition following clock shift.

Three days before the beginning of the training releases a Velcro ring was glued with water-soluble, nontoxic glue to trimmed feathers around the left/right eye of the LH/RH birds, respectively. The complementary piece of Velcro ring was glued to a conical cap made of a double layer of translucent paper (diameter 30 mm), which allowed diffuse light to stimulate the eye, and, therefore, eliminate possible effects on the internal clock. The birds were monitored daily in the loft to observe any possible effect of the monocular occlusion on their behaviour. After monocular occlusion, the birds could feed and drink normally and seemed to get used to wearing the eye cap in a few hours. The LH and RH birds were released as a group with eye caps attached, together with the C birds, near (500 m) their loft to accustom them to flying with one eye covered. The three groups of pigeons together then underwent seven group training releases from each of the two release sites (Livorno, home direction and distance 341°, 12 km; La Sterpaia 194°, 9.5 km), followed by an additional individual release from each training site. Both release sites were 4–5 km from the coast roughly north (La Sterpaia) and south (Livorno) with respect to home. These release sites were chosen such that the sea, constituting a salient topographical feature for reorientation (Gagliardo et al., 2009; Filannino et al., 2014), was on the right side of a pigeon when heading home from La Sterpaia, and on the left side of a pigeon when heading home from Livorno. A consequence of the geographical position of the release sites is that after a fast clock shift (see below) the expected anticlockwise deflection would lead the birds towards the sea when released from Livorno, and inland when released from La Sterpaia.

The GPS loggers were applied to the pigeons before displacement. The pigeons were transported in a crate with a removable