



## A computational model of mapping in echolocating bats



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Echolocating bats can navigate to salient places relying solely on their sonar system. Currently, much about the mechanism underlying sonar-based navigation in bats remains unknown, and no computational models of this ability have been proposed. In this paper, we propose a computational model of sonar-based navigation in bats. In particular, we advance a model explaining how bats could assemble a cognitive map from their environment using only their sonar readings. The model consists of two loops. The first loop performs low-level obstacle avoidance. This gives rise to stable and environment-derived flight corridors (i.e. preferred pathways for bats flying through the environment). The second high-level loop runs on top of the low-level loop and performs mapping. Mapping is done by combining local view information extracted from echo signals with local self-motion information to recognize previously visited places and memorize their spatial relationships. Using this model, we simulate a bat exploring unstructured environments while constructing a cognitive map using a biologically plausible algorithm. The model we propose allows the simulated bat to construct a global map of its flight paths through the environment without the bat ever reconstructing the three-dimensional layout of the local environment from any of its received echo signals. Indeed, neither the obstacle avoidance strategy that guides the bat through space nor the mapping algorithm requires the three-dimensional geometric structure of the environment to be accessible to the bat.

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Echolocating bats can navigate to salient places (Schnitzler, Moss, & Denzinger, 2003) relying solely on their sonar system. Indeed, bats deprived of sight have been found to successfully return to their roost when displaced by up to about 60 km (Davis & Barbour, 1970; Mueller & Emlen, 1957; Stones & Branick, 1969; Williams, Williams, & Griffin, 1966). Also, bats exploring completely dark flight cages have been shown to retain spatial memory over long periods of time (Barchi, Knowles, & Simmons, 2013). Moreover, as in other mammals (Derdikman & Moser, 2010), place cells have been found that encode the bat's location while echolocating (Ulanovsky & Moss, 2007; Yartsev & Ulanovsky, 2013). Currently, much about the mechanism underlying sonar-based navigation in bats remains unknown (Holland, 2007; Geva-

Sagiv, Las, Yovel, & Ulanovsky, 2015) and no computational models of this ability have been proposed.

In this paper, we advance a computational model explaining how bats could assemble a cognitive map representing the global layout of the flight corridors in their environment using only sonar readings. The concept of a cognitive map has been employed differently by various authors (Bennett, 1996). However, here we use its original definition as a global spatial representation of the animal's environment (Tolman, 1948). We propose the bat constructs first a topological map (Franz & Mallot, 2000; Trullier, Wiener, Berthoz, & Meyer, 1997) representing only neighbourhood relationships (i.e. a graph representation with nodes corresponding to distinct places and edges to specific motor programmes), which is subsequently and gradually augmented with metric information (i.e. distances and directions), as the bat revisits the same distinct places. We have called such maps of the environment augmented topological maps (Peremans & Vanderelst, 2013) and referred to them as semimetric maps because the accuracy of the metric information associated with the nodes varies across the graph. For less-travelled parts of the

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environment, the metric information can be unreliable, and the map is still mostly a topological map. For well-explored parts of the environment, the metric information can be used for optimizing paths: for instance, in calculating shortcuts. As such, the model presented here is intended to model bats engaged in ‘middle-scale navigation’ as introduced in [Schnitzler et al. \(2003\)](#).

The proposed model is based on two assumptions. First, we assume that, while exploring a novel environment, purely reactive sensorimotor loops guide the bat ([Vanderelst, Holderied, & Peremans, 2015](#)). Second, we assume that bats can recognize a place in the environment without reconstructing its local three-dimensional spatial layout ([Vanderelst, Steckel, Boen, Peremans, & Holderied, 2016](#)). The first assumption is based on the observation that many bats follow distinct routes when commuting between roosts and feeding grounds, travelling along the edges of landscape structures on flyways that show high spatial constancy ([Holderied, Jones, & von Helversen, 2006](#); [Schaub & Schnitzler, 2007](#); [Verboom, 1998](#); [Schnitzler et al., 2003](#)). In a previous paper ([Vanderelst et al., 2015](#)), we presented a simple obstacle avoidance algorithm, capable of steering a bat away from obstacles in both two-dimensional and three-dimensional environments. In addition to avoiding collisions, this mechanism also constrains the bat’s movement through the environment, causing it follow a limited set of routes among all the possible ones through a given environment. The second assumption derives from the observation that the ability of cruising bats to reconstruct a three-dimensional geometrical model of the local environment from sonar echoes is inherently limited by the (1) field of view ([Jakobsen, Brinkløv, & Surlykke, 2013](#); [Jakobsen, Ratcliffe, & Surlykke, 2013](#); [Surlykke, Ghose, & Moss, 2009](#)), (2) update rate ([Holderied et al., 2006](#); [Seibert, Koblitz, Denzinger, & Schnitzler, 2013](#)) and (3) temporal resolution of their sonar system ([Simmons, Freedman, Stevenson, Chen, & Wohlgenant, 1989](#); [Surlykke & Bojesen, 1996](#); [Wiegrebe & Schmidt, 1996](#)). As an alternative to three-dimensional geometric reconstructions, we investigated the discriminative power of echo signatures extracted from a large body of sonar echoes collected in real bat habitats ([Vanderelst et al., 2016](#)). An echo signature is a biologically plausible range–energy representation of a sonar echo extracted by calculating the envelopes of the outputs of a cochlear filterbank, dechirping these outputs and summing over the frequency channels. In brief, an echo signature is a coarse range–energy (or, time–energy) representation of the echo. Our main result is then to show, using numerical simulations, how a robust mapping capability arises out of the interactions of this low-level reactive behaviour with the echo signature-based place recognition mechanism.

## THE MAPPING MODEL

A problem central to building a cognitive map (and navigation in general) is the fact that path integration measurements are typically noisy. If path integration (also referred to as odometry) were free of errors, building a cognitive map would be trivial since the egomotion trace could be used directly to form a cognitive map of the environment ([Thrun & Leonard, 2008](#)). Unfortunately, both systematic and random errors accumulate rapidly ([Cheung & Vickerstaff, 2010](#); [Merkle, Rost, & Alt, 2006](#); [Thrun & Leonard, 2008](#)), thereby prohibiting the direct use of the egomotion. Therefore, building an accurate cognitive map requires an animal to have a method for correcting accumulated path integration errors.

In robotics, correcting path integration errors is usually done by averaging the noisy odometry estimates across subsequent travels between places ([Thrun & Leonard, 2008](#)). For large robots in confined spaces (or with long perceptual ranges, [Williams, Dissanayake, & Durrant-Whyte, 2001](#)), this has been shown to be

a feasible approach (e.g. [Steckel & Peremans, 2013](#); [Milford, Wyeth, & Prasser, 2004](#)). The constraints imposed by the environment ensure the robot travels along a limited number of paths. This results in the robot encountering the same places multiple times. This allows the robot to accumulate a sufficient number of replications for a given path between two places. Over time, this leads to a faithful representation of the spatial relationship between places.

For small animals (or robots) this approach is problematic. However, small and agile navigators can follow many paths as the environment does not constrain their motion to the same degree as it does for larger agents. Therefore, it is not guaranteed that the agent will re-encounter the same places ever again. For echolocating bats, the issue is further aggravated by their limited perceptual range ([Stilz & Schnitzler, 2012](#)), their small aperture angle ([Jakobsen, Ratcliffe, et al., 2013](#); [Vanderelst et al., 2010](#)) and the fact that echoes are aspect-angle dependent (e.g. [Yovel, Stilz, Franz, Boonman, & Schnitzler, 2009](#)). This implies that, for a bat to recognize the echo signature of a place it has visited before, its position and orientation have to be somewhat similar to what they were during its previous visit. This is much less so for navigators with wide-aperture sensors, such as robots or insects with omnidirectional vision ([Lambrinos, Möller, Labhart, Pfeifer, & Wehner, 2000](#)).

In summary, mapping requires robust place recognition to integrate measurements across different encounters of the same places ([Kuipers, 2000](#)). Also, because echoes are highly dependent on the location and orientation of a bat, any mechanism that limits the possible positions and orientations of a bat would facilitate the construction of a cognitive map by guaranteeing the bat revisits the same places multiple times.

## Place Recognition

Navigating and route-following require animals to recognize previously visited places ([Franz & Mallot, 2000](#); [Kuipers, 2000](#); [Trullier et al., 1997](#)). While it is evident bats can identify places based on sonar (e.g. [Barchi et al., 2013](#); [Jensen, Moss, & Surlykke, 2005](#)), it is largely unknown how they do this ([Schnitzler et al., 2003](#)), and different mechanisms are possible ([Geva-Sagiv et al., 2015](#)). It has been suggested that bats make use of the reconstructed local three-dimensional geometrical structure to recognize places (e.g. [Clare & Holderied, 2015](#); [Lewicki, Olshausen, Surlykke, & Moss, 2013](#)). While we agree that this hypothesis is sufficient to explain place recognition, we argue that it accounts insufficiently for the limitations of the bat sonar system. More importantly, it is not necessary.

As an alternative to the assumption that bats reconstruct the three-dimensional layout of the environment, we recently proposed that bats directly use the cochlear output ([Vanderelst et al., 2016](#)), extending the template-based classification approach described by [Wiegrebe \(2008\)](#) and [Kuc \(1997a, 1997b, 1997c\)](#). Under this hypothesis, bats are assumed to match the output of the cochlea to a set of stored templates (i.e. recognizing the echo signature of previously visited places), obviating the need for complex reconstruction algorithms extracting three-dimensional spatial information from the echo signals at the two ears. As it uses the sensory input directly, this approach to place recognition is analogous to the view-based place recognition that is thought to underlie visual navigation in many insects ([Graham, 2010](#); [Zeil, Hofmann, & Chahl, 2003](#)). In addition to circumventing the computationally hard problem of deriving a three-dimensional spatial representation from complex echo signals, robotic experiments have shown such acoustic templates to be highly discriminative ([Steckel, Boen, & Peremans, 2013](#)). In a convincing demonstration of the power of this approach, [Kuc \(1997c\)](#) showed a

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