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All roads lead to Rome, even in African savannah elephants—or do they?

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Polansky *et al.*'s [1] investigation of the movement behaviour of African savannah elephants uses advanced technology to track precise movement patterns of the species across large spatial scales. Their findings, specifically the direct movement trajectories taken by these elephants to access waterholes, are suggestive of spatial memory strategies as observed in humans. Polansky *et al.* importantly highlight the robust hippocampal structures of African savannah elephants. Taken together, these two observations may be considered in light of the literature to support spatial memory as the mechanism by which African elephants navigate their habitat.

But do all roads lead to waterholes? Could there be confounding factors such as additional navigational information present leading African elephants to their destination? The mechanisms and neural correlates associated with spatial memory are well explored in humans and may serve as a basis for interpreting the navigation patterns observed in non-human subjects. In 1978 John O'Keefe & Lynn Nadel [2] hypothesized that spatial memory was dependent on the hippocampus. Their work characterized the differences between maps and routes: the former representing curiosity-driven, flexible and efficient information storage with very large capacity for content, and also manipulation. According to O'Keefe and Nadel, detailed maps are built slowly (p. 89). The characteristics of manipulation and flexibility are precisely what allows the prediction that novel trajectories to a target destination can be derived from a cognitive map. Accordingly, the process of deriving information from cognitive maps is relatively slow, confirmed with experimental evidence decades later [3]. Routes, on the other hand, were characterized as target-driven, they are rigid, contain little data and cannot be manipulated. Once learned, routes involve very little decision-making processes and as such become fast and efficient. Cognitive maps are linked to the use of a spatial strategy dependent on the hippocampus, whereas routes involve stimulus–response strategies dependent on the caudate nucleus of the striatum [4]. This dichotomy continues to act as an important framework for understanding human navigational strategies [3].

Much evidence now exists to support the relationship between activity and increased grey matter in the hippocampus in humans who use spatial strategies [5]. O'Keefe's pioneering research on hippocampus 'place cells' in generating cognitive maps earned him the Nobel Prize in Physiology or Medicine in 2014, along with May-Britt and Edvard Moser, who extended cognitive mapping neural computations to entorhinal 'grid cells'. Together with many others, over the span of four decades, they have further characterized hippocampal cells, elucidating how mammals build cognitive maps.

The use of direct paths to specific landmarks from various starting positions, in the case of African elephants, implies the existence of cognitive maps and is considered a hallmark of hippocampus-dependent spatial memory, as defined by O'Keefe and Nadel in 1978. Maguire *et al.* [6] provided supportive evidence by showing that positron emission tomography activity in the right hippocampus correlates with taking direct paths to a target location when humans navigate in a virtual town, where the relationships between landmarks was previously learned, for example, by finding the grocery store from the cinema. In their investigation of the neural basis for wayfinding versus route following, Hartley *et al.* [7] also showed a correlation between taking direct paths during accurate wayfinding in a virtual town and functional magnetic resonance imaging (fMRI) activity in the hippocampus. In addition, they showed that route following was not associated with fMRI activity in the hippocampus but with the caudate nucleus and that speed was noted during route following.

Further evidence is found in Etchamendy and Bohbot's work which confirms that people who spontaneously use spatial memory strategies, previously shown to rely on the hippocampus [3], also travel shorter distances to targets (evidence of taking a direct path) in a virtual town. Spatial navigators have a stronger performance in the virtual town than response navigators who rely on a series of rigid stimulus–response associations [8]. Further evidence to support the involvement of the hippocampus in taking direct paths comes from a study investigating spatial memory in patients with schizophrenia [9]. Patients with schizophrenia demonstrated poor performance on a wayfinding task, which was associated with decreased grey matter in the right hippocampus. On the other hand, healthy young adult controls who were more successful at completing the task had increased grey matter in the hippocampus. Analogous results were reported in a study of ageing, whereby the volume of the hippocampus correlated with shorter distances to target locations in a virtual town. In summary, travelling straight paths to a target are considered a hallmark of spatial memory and they are found to be dependent on the hippocampus.

On the other hand, Nadel & Hardt [10] have argued that pigeons who take detours and follow highways to travel to their destinations, rather than taking a direct path, do not use cognitive mapping. Nadel and Hardt interpret this finding to mean that pigeons favour the stimulus–response strategy, as opposed to the spatial strategy, because the stimulus–response strategy is less cognitively demanding.

Finally, one might argue that the use of olfactory cues is the mechanism underlying direct paths to waterholes in African savannah elephants. However, as stated by Polansky and colleagues, the lack of seasonal differences in navigational accuracy suggests that olfactory cues, which vary according to the wet and dry seasons, were not the basis for elephant trajectories. In fact, for olfactory cues to be useful, environmental conditions such as dissipation gradients, wind currents and temperature must be relatively stable. Both the human and non-human studies listed above reinforce the conclusion that, in line with popular belief, elephants benefit from the longevity and flexibility of hippocampal-dependent spatial memory.

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