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Neurons including hippocampal spatial view cells, and navigation in primates including humans

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Abstract

A new theory is proposed of mechanisms of navigation in primates including humans in which spatial view cells found in the primate hippocampus and parahippocampal gyrus are used to guide the individual from landmark to landmark. The navigation involves approach to each landmark in turn (taxis), using spatial view cells to identify the next landmark in the sequence, and does not require a topological map. Two other cell types found in primates, whole body motion cells, and head direction cells, can be utilized in the spatial view cell navigational mechanism, but are not essential. If the landmarks become obscured, then the spatial view representations can be updated by self-motion (idiothetic) path integration using spatial coordinate transform mechanisms in the primate dorsal visual system to transform from egocentric to allocentric spatial view coordinates. A continuous attractor network or time cells or working memory is used in this approach to navigation to encode and recall the spatial view sequences involved. I also propose how navigation can be performed using a further type of neuron found in primates, allocentric-bearing-to-a-landmark neurons, in which changes of direction are made when a landmark reaches a particular allocentric bearing. This is useful if a landmark cannot be approached. The theories are made explicit in models of navigation, which are then illustrated by computer simulations. These types of navigation are contrasted with triangulation, which requires a topological map. It is proposed that the first strategy utilizing spatial view cells is used frequently in humans, and is relatively simple because primates have spatial view neurons that respond allocentrically to locations in spatial scenes. An advantage of this approach to navigation is that hippocampal spatial view neurons are also useful for episodic memory, and for imagery.

KEYWORDS

allocentric-bearing-to-a-landmark cells, egocentric to allocentric coordinate transforms, episodic memory, hippocampus, idiothetic update, navigation, place cells, spatial view cells

1 | INTRODUCTION

How the brain implements navigation is of major interest in neuroscience. There are a number of different strategies, ranging from taxis (approach) to a viewed goal or to a landmark near a viewed goal, to computations using topological maps that imply knowing the place where one is located, the place of the goal, and performing computations within the topological map utilizing in addition information such as heading, distance travelled, and bearings to landmarks to make use of the map (Ekstrom & Isham, 2017; Franz & Mallot, 2000; Trullier, Wiener, Berthoz, & Meyer, 1997). Here, I propose how navigation can be performed in primates and humans using spatial view cells found in the hippocampus and parahippocampal gyrus. The navigation involves movements to a sequence of landmarks guided by spatial view cells. Interesting aspects of this type of navigation are that a topological map of space is not needed, and the starting place need not be specified as the individual just needs to approach the first landmark to get started. The navigator might utilize a set of instructions such as look for and go towards the church, then look for and go towards the bookshop, and then look for and go towards the College, and that is the goal. It is suggested that this type of navigation, for which spatial view cells provide the foundation it is proposed here, is the most common type of navigation in humans, and is often used when instructions are used to reach a goal.

It is also proposed how navigation using spatial view cells can still continue when the view details are obscured, by using idiothetic (self-motion) update of spatial view cells performed in the dorsal visual system (Section 3.4) which requires transforms from egocentric retinal to allocentric spatial view coordinates (Section 2.6).

In addition, there is some evidence for "allocentric-bearing-to-a-landmark cells" in primates (Dean & Platt, 2006; Snyder, Grieve, Brotchie, & Andersen, 1998), and they are a natural component of the coordinate transforms performed in the dorsal visual system (Rolls, 2020), so a navigational strategy using these is also described, which also does not require a topological map.

Navigation using an internal map of space with places in the map organized to reflect the topology of the space has been a fruitful field of enquiry in neuroscience inspired by the book "The Hippocampus as a Cognitive Map" (O'Keefe & Nadel, 1978), and is supported by the discovery of place cells in the hippocampus of the rat (O'Keefe & Dostrovsky, 1971) and macaque (Rolls & O'Mara, 1995), and grid cells in the entorhinal cortex (Fyhn, Molden, Witter, Moser, & Moser, 2004) of the rat. Schemes have been devised about how this internal map of places in the world and their relative positions can be used with head direction cells to account for navigation (Bicanski & Burgess, 2018; Edvardsen, Bicanski, & Burgess, 2020; Hartley, Lever, Burgess, & O'Keefe, 2014).

But is that how humans generally navigate? What I argue here is that with the great development of the primate visual system, navigational strategies frequently make use of the visual inputs to navigate using distant visual landmarks, and this appears to be characteristic of humans (Waller & Lippa, 2007). In contrast, in rodents navigation may be more based on the place where the rodent is located, with olfactory and somatosensory cues of importance in specifying the place where the rodent is located during navigation which may frequently be in the dark. Indeed, many of the differences between primates and rodents in the representations of space in the brain are related to the great development of the primate visual system (Rolls & Wirth, 2018), which has a high resolution fovea which is used to fixate on different parts of a scene, and a highly developed ventral visual cortical stream specialized for the recognition of objects in natural scenes (Afraz, Yamins, & DiCarlo, 2014; Rolls, 2012; Rolls, 2021; Rolls, Aggelopoulos, & Zheng, 2003), and also for representing scenes themselves (Epstein & Baker, 2019; Epstein & Julian, 2013; Kamps, Julian, Kubilius, Kanwisher, & Dilks, 2016; Kornblith, Cheng, Ohayon, & Tsao, 2013; Nasr et al., 2011). In addition, the highly developed dorsal visual stream of primates has systems for the generation of saccades to fixate parts of scenes and objects in scenes, and to implement update of spatial representations when self-movements are made (idiothetic update; Graf & Andersen, 2014; Galletti & Fattori, 2018; Rolls, 2020). Associated with this great development of the primate visual system for viewing scenes and for finding and remembering where objects are in a scene, neurons specialized for viewing scenes and for objects in scenes are found in the primate hippocampal system (Georges-François, Rolls, & Robertson, 1999; Rolls, Robertson, & Georges-François, 1997; Rolls & Wirth, 2018; Rolls & Xiang, 2006; Wirth, Baraduc, Plante, Pinede, & Duhamel, 2017), with some in the related parietal areas (Dean & Platt, 2006; Rolls, 2020; Snyder et al., 1998).

The plan of the article is that Section 2 describes the properties of these visual spatial and related neurons in primates, as they provide the foundation for the new hypotheses and theory about the implementation of navigation in primates developed and set out in Section 3. Section 4 describes computational models implemented in Matlab to illustrate how navigation in primates including humans could be implemented according to the new hypotheses and utilizing the spatial neurons found in primates. Section 5 presents the results of the simulations of the models. In Section 6, implications of the new approaches to the implementation of some navigational strategies in primates including humans are described.

2 | PREMISES TO THE THEORY: THE PROPERTIES OF THE TYPES OF SPATIAL NEURON FOUND IN THE HIPPOCAMPAL AND RELATED SYSTEMS IN PRIMATES

2.1 | Spatial view neurons

In macaques, spatial view neurons respond to a location in space "out there" at which the primate is looking, and are present in the hippocampus and parahippocampal gyrus (Georges-François et al., 1999; Robertson, Rolls, & Georges-François, 1998; Rolls et al., 1997; Rolls & O'Mara, 1995; Rolls, Treves, Robertson, Georges-François, & Panzeri, 1998). The spatial view neurons fire to a viewed location in space relatively independently of eye position, head direction, and the place where the individual is located, and therefore provide an allocentric representation of viewed space (Georges-François et al., 1999; Rolls et al., 1998). This is important for memory and navigation, for this enables correct recall of the viewed spatial location and the object or

reward or goal at the viewed location in a scene, even if the eye position, head direction, and place are different from when the learning took place previously. The location in a scene at which spatial view neurons fire can be updated for a few minutes by eye and head and walking movements made in the dark, and this may be useful in selecting goals for navigation in the dark (Robertson et al., 1998). This update by self-motion is referred to as idiothetic update. These spatial view cells responded to viewed locations in a rich spatial environment in which the monkey could walk freely and turn the head. The spatial view neurons respond to the location in both the horizontal and vertical planes of the spatial scene at which the monkey is looking, not where the monkey is facing (Georges-François et al., 1999). These spatial view cells are likely to be important in remembering what has been seen where in the environment, in that some spatial view cells respond to a combination of spatial view and object in an "object-to-place in a scene" memory task (Rolls, Xiang, & Franco, 2005), and this may be important in navigation to find an object. Further, some spatial view cells respond to the location of a reward in a scene in a "reward-to-location in a scene" memory task (Rolls & Xiang, 2005), and may therefore be useful in navigation to goals. (Further information about hippocampal spatial view cells, including videos to illustrate their firing during locomotion [Rolls & Wirth, 2018], and coloured firing rate plot versions of the corresponding papers [Rolls et al., 1997; Robertson et al., 1998; Georges-François et al., 1999], are available at https://www.oxcns/org/publications).

Useful confirmation has also recently been obtained that relatively many macaque hippocampal neurons respond to the location "out there" in space towards which the animal is facing (22% of neurons), compared to only 5% of hippocampal neurons that encode the place where the macaque is located (Mao et al., 2020). Some neurons were classified as spatial view cells and others as "facing location" cells, but the environment being viewed was simple (a cylindrical arena with a drain on the floor and two touchscreens with food on the walls), and more spatial view cells are likely to be found in a rich spatial environment such as the open lab that we used (Georges-François et al., 1999; Robertson et al., 1998; Rolls et al., 1997; Rolls et al., 1998). Indeed the reason that we moved to a rich open lab visual environment was that we expected to find, and did find, more spatial view cells than in a relatively simple spatial environment with only four cues in the testing arena (Rolls & O'Mara, 1995). Spatial view cells in our testing environments were found to respond to where the macaque was looking in space, and not to the location towards which the individual was facing, by testing these specific hypotheses (Georges-François et al., 1999; Rolls et al., 1997; Rolls & O'Mara, 1995). Further evidence is that in the dark, spatial view cells respond to a remembered spatial view location only when that location is being looked at, with facing location held constant (Robertson et al., 1998). In terms of brain computations, it makes sense for spatial view cells to respond to viewed locations in a natural scene that has many useful and clear landmarks, even if an individual is not facing those locations but is looking at them, because it is where objects or landmarks are in the environment, not where one is facing, that is important for memory and navigation (Rolls, 2021).

Visual hippocampal neurons have also been found in a star maze task in spatial navigation in virtual reality that responded to the location where the macaque looked, though in this task the majority of the neurons responded to the spatial view best from particular places (Wirth et al., 2017). Interestingly, some of these neurons also showed idiothetic update, in that they responded to a location in the scene towards which the macaque moved the eyes even before that part of the scene had appeared on the virtual reality screen (Wirth et al., 2017). In a maze task performed in virtual reality, each spatial view may be seen typically from only some places, and this may contribute to the modulation by place of some neurons that respond to where the macaque is looking (Rolls, 2021).

For humans there is evidence for medial temporal lobe and hippocampal neurons with properties like those of spatial view cells, for example to locations being viewed (from recordings in patients during neurosurgery; Ekstrom et al., 2003; Miller et al., 2013). In the study by Ekstrom et al. (2003), some medial temporal lobe neurons were found to represent views of landmarks. In another study of human medial temporal lobe neurons, it was found that in a Treasure Hunt game, some neurons respond to the sight of remote locations rather than the individual's own place (Tsitsiklis et al., 2020). Just like macaque spatial view cells, these neurons in humans respond when the spatial location is seen with different bearings (showing that they are not "allocentric-bearing-to-a-landmark" neurons, but spatial view neurons). The locations in the human Treasure Hunt game were in at least some cases within the spatial environment that could be viewed. In the macaque testing, hippocampal spatial view neurons could respond when the macaque was distant from an effective part of the 3D environment (e.g., the location in the scene where a trolley was located), but also when the macaque was close to the effective part of the environment (e.g., at the place where the trolley was located, as illustrated by Rolls [Rolls, 1996, 2021]). This is thus somewhat comparable to the way in which the human visual "spatial target" neurons responded (Tsitsiklis et al., 2020). The results in humans (Tsitsiklis et al., 2020) thus appear to confirm the presence of spatial view cells in humans that were discovered in macaques (Feigenbaum & Rolls, 1991; Rolls et al., 1989; Rolls et al., 1997; Rolls & O'Mara, 1995). Further, in humans some medial temporal lobe neurons reflect the learning of paired associations between views of places, and people or objects (Ison, Quian Quiroga, & Fried, 2015; just as in macaques, Rolls et al., 2005), and this implies that neurons coding for views of scenes are important for human hippocampal function.

Consistent with this, human functional neuroimaging studies do show hippocampal activation when scenes or parts of scenes are viewed even when the human is fixed in one place for neuroimaging (Brown et al., 2016; Brown, Ross, Keller, Hasselmo, & Stern, 2010; Burgess, 2008; Chadwick, Hassabis, Weiskopf, & Maguire, 2010; Chadwick, Mullally, & Maguire, 2013; Epstein & Kanwisher, 1998; Hassabis et al., 2009; Maguire, 2014; O'Keefe, Burgess, Donnett, Jeffery, & Maguire, 1998; Zeidman & Maguire, 2016).

In rodents some hippocampal and related retrosplenial neurons can be influenced by visual stimuli such as lines or patches (Acharya, Aghajan, Vuong, Moore, & Mehta, 2016; Chang et al., 2020; Fischer, Mojica Soto-Albors, Buck, & Harnett, 2020; Mao, Molina, Bonin, & McNaughton,

2020), but given the absence of a fovea and of eye movements to fixate a location in a scene, it is not yet known how similar these neurons are to the spatial view cells of primates, which respond when the primate fixates at a particular location in space from different places.

2.2 | Allocentric-bearing-to-a-landmark neurons

Neurons that appear to respond to an allocentric (world-based) bearing to a visual stimulus have been described in the macaque parietal cortex area 7a (Snyder et al., 1998) and in the posterior cingulate cortex (which receives inputs from the parietal cortex including area 7a; Dean & Platt, 2006). These neurons respond to a location in space independently of the angle with respect to the body or head when these are rotated, and thus represent bearings with respect to the macaque in allocentric (world-based) not egocentric coordinates. These neurons could be involved in encoding bearings to landmarks (although testing in different places is needed to show whether they encode bearings or spatial view (cf. Feigenbaum & Rolls, 1991; Georges-François et al., 1999). Consistent with the hypothesis that they encode bearings to landmarks, some primate hippocampal neurons respond when the macaque looks at a spatial view, a landmark, but from only some places in a virtual reality environment (Wirth et al., 2017). Moreover, in humans some hippocampal system neurons may have responded to bearings to landmarks (Ekstrom et al., 2003). In the rodent entorhinal cortex, some neurons respond to bearings to objects (Deshmukh & Knierim, 2013; Hoydal, Skytoen, Andersson, Moser, & Moser, 2019), and it is possible that the rodents were treating the objects like landmarks. Another reason for considering allocentric-bearing-to-a-landmark neurons is that they are naturally generated in a theory and model of coordinate transforms in the primate dorsal visual system (Rolls, 2020).

2.3 | Whole body motion cells

Two principal types of neuron in the primate hippocampal system provide idiothetic (self-motion) information useful for navigation. The first type of neuron is hippocampal whole body motion cells (O'Mara, Rolls, Berthoz, & Kesner, 1994). Some of these neurons respond to linear translation and others to (angular) head rotation. Some of these neurons respond to vestibular cues, others to the corresponding visual cues for optic flow, and some to both. The vestibular inputs are evident when the movements are in the dark. In the light, rotation of the environment to produce optic flow was able to activate some of these neurons. Some of this testing was performed while the monkey was moved on a robot (O'Mara et al., 1994). It is neurons that respond to vestibular inputs that are important for idiothetic update in the dark. Of course, the visual cues produced by the corresponding motion may be used for idiothetic navigation in the light (O'Mara et al., 1994). The neurons are found in both the primate hippocampus and subiculum (O'Mara et al., 1994). There may be similar neurons to those we discovered in primates (O'Mara et al., 1994) found more recently in rodents in the medial entorhinal cortex termed "speed cells" which respond to translation (i.e., linear motion; Kropff, Carmichael, Moser, & Moser, 2015; Hinman, Brandon, Climer, Chapman, & Hasselmo, 2016), and neurons that respond to angular velocity (i.e., head rotation) have also been described in the rat parietal cortex (Wilber, Clark, Forster, Tatsuno, & McNaughton, 2014; Wilber, Skelin, Wu, & McNaughton, 2017), but the roles of visual versus vestibular inputs for these rodent neurons are not yet clear. In primates, neurons in parietal cortex area 7a can respond to vestibular and/or visual cues of self-motion (Avila, Lakshminarasimhan, DeAngelis, & Angelaki, 2019; Bremmer, Duhamel, Ben Hamed, & Graf, 2000; Cullen, 2019; Wurtz & Duffy, 1992). A similar system may be present in humans, with activations found to optic flow in V3A which has functional connectivity with the hippocampus (Sherrill et al., 2015), where we discovered hippocampal neurons sensitive to optic flow (O'Mara et al., 1994). These inputs may reach the hippocampus via the parahippocampal gyrus area TH, which in humans has direct connections with these parietal areas, early visual cortical areas, and with the hippocampus (Huang, Rolls, Hsu, Feng, & Lin, 2021; Qing, Rolls, Huang, Cheng, & Feng, 2021; Rolls, Deco, Huang, & Feng, 2021).

2.4 | Head direction cells

The second principal type of neuron in primates that provides idiothetic information useful for navigation is head direction cells, well known in rodents (Cullen & Taube, 2017; Taube, Muller, & Ranck Jr., 1990), which we discovered in the primate presubiculum (Robertson, Rolls, Georges-François, & Panzeri, 1999; and they are probably elsewhere). These neurons continue to encode head direction even when the monkey is moved from a familiar room to a relatively unfamiliar corridor, and maintain their directionality for a few minutes in the dark, after which they drift. This is important, for these cells can only maintain head directionality for a relatively short period without visual cues to lock them back into the correct directionality. Their inputs are derived from velocity signals produced in the vestibular nuclei in the brainstem and reach the parietal vestibular cortical areas (Cullen, 2019; Grusser, Pause, & Schreiter, 1990; Ventre-Dominey, 2014). The direction signal thus reflects a great deal of integration over time, and this is imprecise and noisy resulting in drift. This means that only short-term idiothetic navigation (i.e., without visual cues) is possible. Vestibular signals influence neurons in a number of parietal cortex areas including VIP, with neurons that respond to head position (i.e., head direction) or head acceleration, in addition to the many neurons with head velocity tuning (Klam & Graf, 2003). Neurons that respond to vestibular inputs produced by head rotation or translation are also found in area 7a (Avila et al., 2019). The parietoinsular vestibular cortex may be especially important in the sense of direction (Chen, Gu, Liu, DeAngelis, & Angelaki, 2016).

2.5 | Place cells

Neurons have been discovered that respond in a cue-controlled environment to the place where the macaque was located, to movement

to a place, or to spatial view depending on the place where the monkey was located (Rolls & O'Mara, 1995). Macaque hippocampal neurons that respond to place have also been described in virtual navigation tasks (Furuya et al., 2014; Wirth et al., 2017) and have also been reported in marmosets (Courellis et al., 2019). Place cells that respond in virtual navigation to the place in virtual space have also been described in the human hippocampus, with other neurons responding like spatial view cells to the locations of viewed landmarks (Ekstrom et al., 2003).

2.6 | Coordinate transforms in the dorsal visual system useful for idiothetic navigation in primates: From retinal position to head-centred coordinates, then allocentric-bearing-to-a-landmark, and then to allocentric spatial view coordinates

Eye position is in head-based, egocentric coodinates. If the location in space at which we are looking is to be interfaced to the allocentric spatial view system, then a series of coordinate transforms is needed, to convert the egocentric representation on the retina to allocentric spatial view representations, to enable idiothetic navigation towards the landmark even when the view is obscured. It has been proposed that the primate dorsal visual system is used for idiothetic update of spatial view cells and allocentric-bearing-to-a-landmark cells (Rolls, 2020). These coordinate transforms and the proposed underlying mechanisms are summarized next and illustrated in Figure 3.

Figure 1 shows that the first transform is from retinal position to head-based (egocentric) position in space, which is performed by gain modulation using eye position in LIP and VIP (Salinas & Abbott, 2001; Salinas & Sejnowski, 2001). It was found that adding to gain modulation a trace learning rule of the type implemented in the ventral visual system (Rolls, 2012; Rolls, 2021) enables the invariant representations to be learned better at every stage of the system (Rolls, 2020).

The second coordinate transform is from egocentric head-based coordinates to allocentric-bearing-to-a-landmark coordinates, using gain modulation by head direction (Rolls, 2020). Neurons that fit this description are found in the macaque parietal cortex 7a (Snyder et al., 1998) and the posterior cingulate cortex (Dean & Platt, 2006; Figure 3).

The third coordinate transform is from the "allocentric-bearing-to-a-landmark" representation into an allocentric spatial view

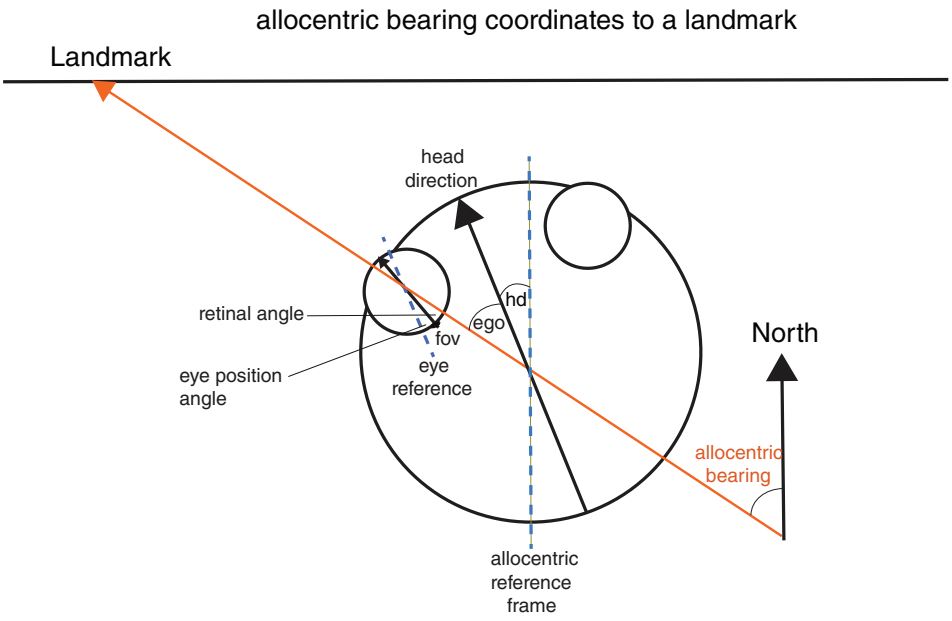

FIGURE 1 Representation of an allocentric-bearing-to-a-landmark. The large circle is the head, and the two small circles are the eyes. The allocentric bearing to the landmark is given by the angle between North and the red line from the individual (observer) to the landmark. In this case the allocentric reference frame (indicated by the blue dashed line) is aligned with North, but it could be specified by dominant environmental cues in a particular environment. The large black arrow labelled "head direction" specifies the direction relative to the allocentric reference framework in which the head is facing, with the head direction angle "hd" as shown. The head direction (hd) is thus in allocentric coordinates. The egocentric bearing to a landmark ("ego") is the angle between the head direction and the line of sight to the landmark (As the diagram makes clear, combining the egocentric bearing of the landmark and the head direction yields the allocentric-bearing-to-a-landmark). The diagram also shows how the eye position (the angle between the eye reference frame which is aligned with the head direction as shown), and the retinal angle (the angle between the fovea ["fov"] and the place on the retina of the image of the landmark) are relevant. Gain modulation can be used at three stages of the primate dorsal visual system to perform idiothetic update over different eye positions, and head directions to compute allocentric bearings to a landmark, but also over different places to compute where the observer is looking in the scene as encoded by spatial view cells (Rolls, 2020). "Allocentric-bearing-to-a-landmark" neurons respond when a particular landmark is at a particular allocentric bearing. "Spatial view cells" are different, in that their responses are relatively invariant with respect to the bearing to the landmark, and therefore of the place where the viewer is located (Georges-François et al., 1999) [Color figure can be viewed at wileyonlinelibrary.com]

representation by gain modulation using translation of the animal to different places (Rolls, 2020; see Figure 3).

This builds a representation in the same spatial coordinates used in the primate hippocampus, namely allocentric spatial view that represents a location in allocentric space "out there", independently of the exact place where the individual is located, as well as its head direction and eye position. This type of representation is ideal for the episodic memory functions of the primate hippocampus, for it enables memories to be formed of where in allocentric space an object or person was seen. Because the memory is independent of the exact place where the individual is located, if the same location is seen from a different place, the hippocampal memory system will correctly recall the object or person that was at that location. Similarly, if the object or person is the recall cue, the location in allocentric space where they were seen can be recalled from the CA3 network in the hippocampus, and that memory is suitable for navigation to that location, because it does not depend on the place where the animal is, which would be very restrictive indeed in a memory system (Rolls, 2018; Rolls, 2020).

These primate dorsal visual system coordinate transforms are used in the model of navigation described below involving idiothetic update of spatial view cell representations, to enable navigation when the view details are obscured or when in the dark.

(The rodent has a much less well developed visual system than primates and may have no posterior cingulate cortex (Vogt, 2009), but reference should be made to the egocentric boundary vector tuning of neurons in the retrosplenial cortex (Alexander et al., 2020).)

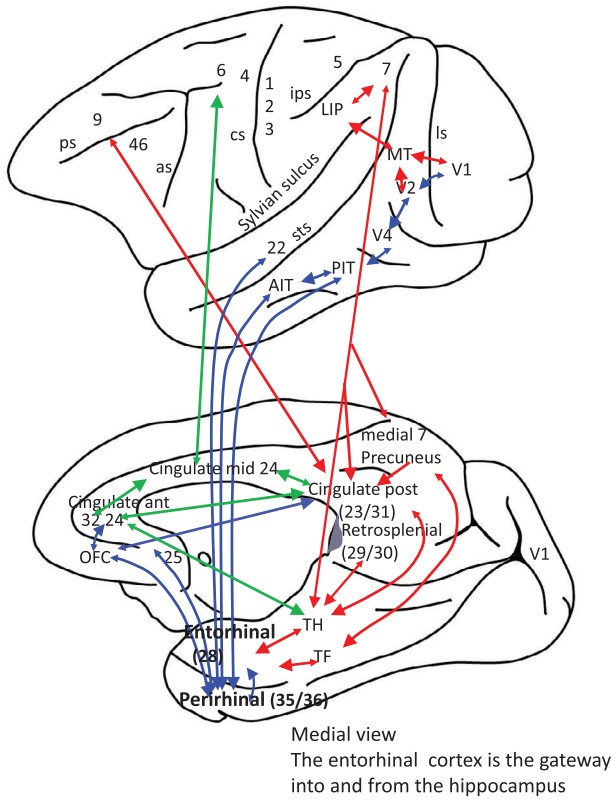

FIGURE 2 Legend on next coloumn.

3 | THEORY: THE NEW HYPOTHESES ABOUT HOW NAVIGATION COULD BE IMPLEMENTED USING SPATIAL NEURONS OF THE TYPE FOUND IN PRIMATES

Hypotheses about how four types of navigation could be implemented in primates based on the types of spatial neuron found in primates are presented in this section.

3.1 | Navigation using spatial view cells

The hypothesis is that navigation can be implemented by movements to a sequence of landmarks, with each landmark encoded by a different set of spatial view cells. The goal, the last landmark, need not be in sight. At the end of each leg of the route,

FIGURE 2 Cortical connections of the primate hippocampus showing how it receives inputs from the ventral processing streams (blue) and the dorsal processing streams (red). It is argued in this article that idiothetic update of hippocampal spatial view representations, useful for navigation, is computed in the dorsal visual system up through the parietal cortex, posterior cingulate, and retrosplenial cortex. Object information reaches the hippocampus from the temporal cortex parts of the ventral visual system. Visual scene information that drives hippocampal spatial view cells may come from the parahippocampal place area (Epstein & Baker, 2019), and also from the ventral visual stream. The parahippocampal cortex is indicated by areas TF and TH. A medial view of the macaque brain is shown below, and a lateral view is above. The entorhinal cortex area 28 is the main entry for cortical connections to and from the hippocampus. The forward projections to the hippocampus are shown with large arrowheads, and the backprojections with small arrowheads. The main ventral stream connections to the hippocampus that convey information about objects, faces, etc. are in blue, and the main dorsal stream connections that convey "where" information about space and movements are in red. The ventral "what" visual pathways project from the primary visual cortex V1 toV2, then V4, then posterior inferior temporal visual cortex (PIT), then anterior inferior temporal visual cortex (AIT), then perirhinal cortex (areas 35/36), and thus to entorhinal cortex. The dorsal "where" visual pathways project from V1 to V2, then MT (middle temporal), then LIP (lateral intraparietal), then parietal area 7 (lateral) and medial (including the precuneus), then to posterior cingulate cortex areas 23/32) including the retrosplenial cortex (areas 29/30) and thus to parahippocampal gyrus (areas TF and TH), and then perirhinal and entorhinal cortex. Area 22 is superior temporal auditory association cortex. The hippocampus enables all the high order cortical regions to converge into a single network in the hippocampal CA3 region. The retrosplenial cortex (29,30) is the small region in primates including humans behind the splenium of the corpus callosum shaded grey: it is not necessarily homologous with what is termed retrosplenial cortex in rodents (Vann, Aggleton, & Maguire, 2009), which may also not have a homologous posterior cingulate cortex (Vogt, 2009). Other abbreviations: as-arcuate sulcus; cs-central sulcus; ips-intraparietal sulcus; ios-inferior occipital sulcus; ls-lunate sulcus; sts-superior temporal sulcus (modified from Rolls & Wirth, 2018) [Color figure can be viewed at wileyonlinelibrary.com]

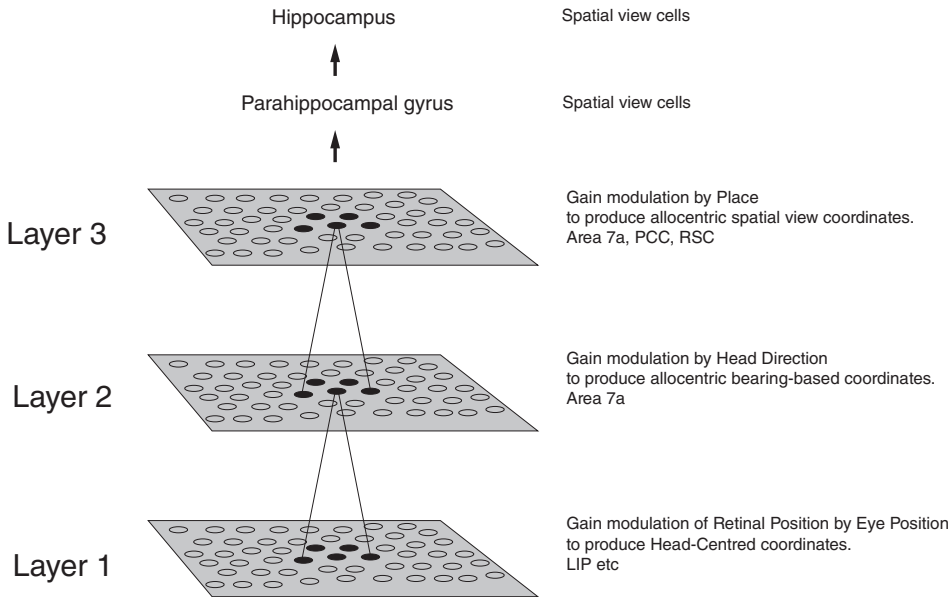

FIGURE 3 Coordinate transforms in the primate dorsal visual system. Three principal computational stages of coordinate transforms from retinal coordinates via head-centred coordinates and then via allocentric bearing-based coordinates to spatial view coordinates are shown, together with the brain regions in which the different types of neuron are found. The diagram shows the architecture of the VisNetCT model in which gain modulation combined with short-term memory trace associative learning was shown to implement these transforms (Rolls, 2020). Each neuron in a layer (or cortical area in the hierarchy) receives from neurons in a small region of the preceding layer. It is proposed here that idiothetic update through this dorsal visual cortical stream is used for idiothetic update of spatial view cells when the environment may not be visible for short periods within which the idiothetic update is accurate. PCC, posterior cingulate cortex; RSC, retrosplenial cortex

when the landmark is reached, the next landmark in the sequence can be searched for visually by looking around for it, and when it is seen, the next movements are made to approach that landmark.

In more detail, at the starting point the individual looks around for the first landmark using spatial view cells to identify it, and then approaches the landmark by what is termed taxis, a process that does not require maps or bearings or distance travelled or head direction or remembered body turns, and means just moving towards a landmark or goal (Trullier et al., 1997). When that landmark has been reached, the individual looks round and when the second landmark in the sequence is identified with spatial view cells, the individual moves towards that by the same process of taxis. That is repeated until the goal is reached at the last landmark. The sequence of landmarks has to be stored for the navigation, as described next.

The set of instructions could be stored in human working memory, for example, "walk towards Trafalgar Square, and when you reach it, turn right (or South) and walk towards the Houses of Parliament." The sequence could also be stored in a continuous attractor network, which can store not only the topological sequence, but also can have associated at any step the egocentric body turn or allocentric head direction information, as shown previously (Rolls & Stringer, 2005; Stringer, Rolls, & Trappenberg, 2005).

Part of the utility of spatial view cells for this computational role in navigation is that they are largely place invariant, as well as invariant with respect to head direction and eye position (Georges-François et al., 1999), so they are able to guide the individual irrespective of the exact place, head direction, etc. from which the next landmark is viewed. Moreover, if the landmark is temporarily obscured, by a barrier, darkness, etc., then spatial view cells can still be used to guide the individual to the next landmark, because they can be updated for a few minutes by self-motion (Robertson et al., 1998), with the idiothetic mechanism for this using the primate dorsal visual system (Rolls, 2020). A major advantage of navigation using spatial view cells is that this does not require path integration, and so very long routes with many legs can be followed. This is in contrast to navigation using "allocentric-bearing-to-a-landmark" cells using body turns, as shown next.

If this is the first time that a route has been followed by a human, the list of sequential landmarks could be implemented in the hippocampal episodic memory system. The sequence could be stored by using the time-cells (Eichenbaum, 2014; Eichenbaum, 2017; Howard & Eichenbaum, 2015; Kraus, Robinson, White, Eichenbaum, & Hasselmo, 2013; Macdonald, Lepage, Eden, & Eichenbaum, 2011; Salz et al., 2016) generated in the entorhinal-to-hippocampal system (Rolls & Mills, 2019; Rolls, 2021), and associating each landmark with a different time in the time-cell system in the hippocampus. Another possibility is the use of a continuous attractor network for spatial view cells, described previously (Rolls & Stringer, 2005; Stringer et al., 2005). Another possibility is that the sequence of landmarks is stored in short-term/working memory in the prefrontal cortex (Gilbert & Burgess, 2008; Passingham & Wise, 2012; Rolls, 2021).

Each step in the sequence could have additional information associated with it. One example could be that when one landmark is reached, the landmark could be associated with for example "turn right", which is egocentric information, and is available in whole body motion cells in the primate hippocampus (O'Mara et al., 1994; or what appears to be the equivalent, speed cells in rodents [Kropff et al., 2015]). A second example would be "turn South", which is allocentric information, and is available in head direction cells in the primate presubiculum (Robertson et al., 1999). This is exactly the type of information that could be associated together in the primate hippocampus, utilizing especially CA3 pyramidal cells (Kesner & Rolls, 2015; Rolls, 2018). Another type of information that could also be associated with each step of the sequence is the distance to be travelled between the landmarks, which could be implemented by idiothetic update. The idiothetic update mechanisms are described below, and could utilize primate whole body motion cells (O'Mara et al., 1994) and primate head direction cells (Robertson et al., 1999).

If the route becomes well learned, and is implemented by a continuous attractor network in the hippocampus, which would implement the spatial views as being adjacent in the sequence because of overlap of the spatial view fields (Rolls, 2016a; Rolls & Stringer, 2005; Stringer et al., 2005), each step of the continuous attractor could have additional information associated with it, in the way just described.

3.2 | Navigation using allocentric-bearing-to-a-landmark cells

The hypothesis is that navigation could utilize the "allocentric-bearing-to-a-landmark" cells by combining these cells with whole body motion or head direction cells to determine the direction of travel. For each leg of the route, the individual moves in a particular direction, using head direction cells; or using a starting direction and whole body motion cells that code for rotation to ensure that the path is straight without rotation; or both. When a particular landmark has a particular bearing, the next leg of the route starts by changing to a new direction of travel specified by (allocentric) head direction cells, or by (egocentric) whole body motion cells. The goal, the last landmark, need not be in sight. A sequence of instructions that could be stored in human working memory for the navigation might be: "First proceed West until the Eiffel Tower bears North; then, second, turn South, and proceed until you see a bank bearing West; and then third …" But the instruction might equally be framed with egocentric body turns, as it is only the bearing to the landmark that is allocentric: "First proceed straight in that direction (pointed to) until the Eiffel Tower bears North; then, second, turn right and proceed until you see a bank bearing West; and then third …" The sequence could also be stored in a continuous attractor network, which during previous navigation of the route can associate not only the sequence of allocentric bearings, but also can have associated at any step the egocentric body turn or allocentric head direction information for the turn needed at the start of the next leg when the bearing is reached.

The interest of this type of navigation is that it involves navigation via and to places that are not at landmarks, and uses just two types of neuron found in primates, allocentric-bearing-to-a-landmark cells, and head direction or whole body motion cells.

If the distance to a landmark is part of what is encoded by "allocentric-bearing-to-a-landmark" cells, then this is helpful, though not essential. In rodents, cells that reflect the bearing and distance to an object have been described (Hoydal et al., 2019), and the primate equivalent that would be useful in navigation is "allocentric-bearing-to-a-landmark vector" cells that encode distance as well as allocentric bearing.

If more than one "allocentric-bearing-to-a-landmark" cell is used at any one time in this type of navigation, then the navigation can be thought of as navigation from place to place, where each place is defined by a combination of active "allocentric-bearing-to-a-landmark" cells, and this is described in the following section in which triangulation is used.

This type of navigation is restricted to relatively short trajectories when whole body motion cells are being used for turns at each waypoint and to not turn apart from that, as the path integration required to maintain whole body motion cells is likely to last for only a few minutes, as it relies on integration over signals such as vestibular and proprioceptive input or corollary discharge. Further, the neurons that encode allocentric-bearing-to-a-landmark are only likely to be able to function usefully for a period within which the sense of direction can be maintained by distant landmarks, for the allocentric bearing must be with respect to a maintained allocentric frame of reference. This is in strong contrast with navigation using spatial view cells, which do not rely on any sense of direction or on body movements being remembered and continuously updated. That is a major advantage of navigation using spatial view cells.

A topological map is not necessary for navigation using bearing-to-a-landmark cells, for it does not require geometrical calculation in a Euclidean space, but instead use of a sequence of bearings to landmarks, and whole body motion or head direction cells.

3.3 | Navigation using combinations of allocentric-bearing-to-a-landmark cells: Triangulation

Combinations of active "allocentric-bearing-to-a-landmark" cells represent a place. Navigation using this type of triangulation is harder to implement in the brain, but is practiced by mariners, and was simulated as follows for comparison with the navigational strategies previously described. The environment is formulated computationally as a Euclidean allocentric topological space as envisaged for rodent place cells (O'Keefe & Nadel, 1978) and in many models of navigation in rodents (Bicanski & Burgess, 2018; Edvardsen et al., 2020; Hartley et al., 2014), with X and Y coordinates to define each place.

To move from place to place, the individual calculates its place at every small step of the locomotion by triangulation, using combinations of the active "allocentric-bearing-to-a-landmark" cells. The individual then calculates the (allocentric) compass bearing to the next

place using its current X,Y position, and its knowledge of the X,Y position of the next place, and uses that bearing as the navigational heading, and moves in the direction of that heading. Once the place of the next waypoint is reached, the sequence generator loads the X,Y coordinates for the next leg, and navigation continues.

This type of navigation works if a topological map is stored in the head, and if trigonometric calculations can be performed, and may not be biologically plausible without the ability to triangulate and to calculate directions for the next heading in a topological map. A major disadvantage of this type of navigation is that it can only be performed for as long as "allocentric-bearing-to-a-landmark" neurons can be updated by path integration to maintain a stable sense of direction, or with the use of a compass. If the allocentric-bearing-to-a-landmark cells are reset by a view of the environment as head direction cells can be in rodents (Cullen & Taube, 2017) and primates (Robertson et al., 1999), then if a dominant landmark enables a stable sense of direction to be maintained, bearings to other landmarks might still be useful for navigation.

This type of navigation by triangulation is thus very different from that performed using spatial view cells, which does not require trigonometry in a Euclidean topological space. This type of trigonometric navigation is considered here, so that it can be contrasted with the types of navigational strategy afforded by the use of spatial view cells and allocentric-bearing-to-a-landmark cells described above. For the reason just given, navigation in primates using spatial view cells or "allocentric-bearing-to-a-landmark" cells as described in the previous two sections, *or combinations of these two approaches*, are, it is proposed here, more likely, and more commonly used in primates including humans, than is triangulation.

3.4 | Idiothetic navigation in primates

A very different strategy for navigation than using visual cues about locations in scenes is idiothetic navigation, that is, navigation based on self-motion. This is an essential strategy in the dark or when visual landmarks cannot be seen. Idiothetic information may also be combined with information based on visual (or for that matter auditory) inputs as part of a navigational strategy. Two of the principal types of neuron in primates that provide idiothetic information useful for navigation are head direction and whole body motion neurons, and are described in Section 2 "Premises to the theory" as they are used in the following idiothetic navigational strategy. It is emphasized that in primates some hippocampal whole body motion cells encode angular rotation, and others linear movement (O'Mara et al., 1994).

Neurons of these two types, head direction and whole body motion, could be used as follows for idiothetic navigation in the dark, or without visible landmarks. We can consider the route illustrated in Figure 5a but performed in the dark without the landmarks visible. If the individual starts off with an Easterly head direction at Waypoint 1, then navigation would use head direction cells to keep the direction constant, and integration over linear whole body motion cells (which encode velocity) to locomote for the distance to Waypoint 2. At Waypoint 2, the sequence generator would have associated with it an egocentric "turn right" signal calibrated by head rotation whole body motion cells; or an allocentric head direction signal to turn to face South. The distance to W3 would then be traversed using integration over the linear whole body motion cells. After the correct distance, the sequence generator would specify an egocentric "turn right" signal calibrated by head rotation

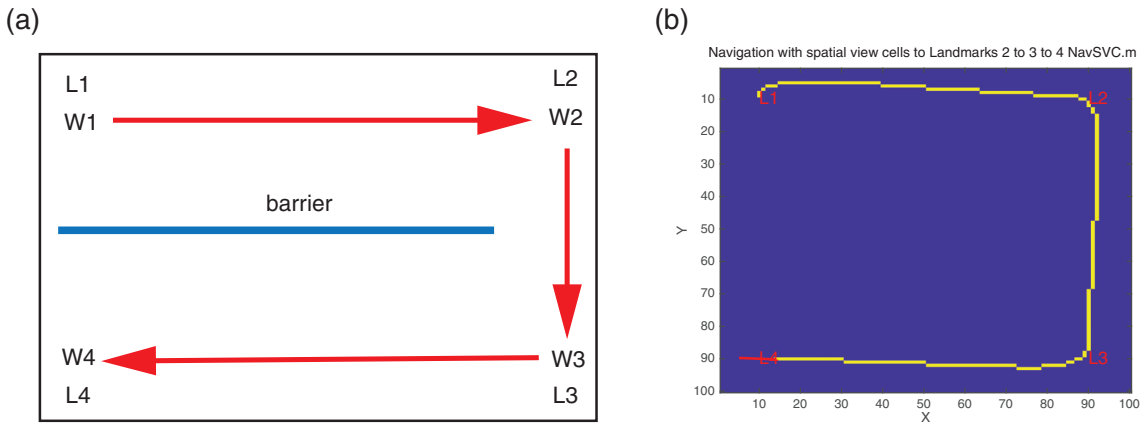

FIGURE 4 (a) An example of navigation using spatial view cells. The task is to start at Landmark 1 (L1), and to reach Landmark 4 (L4). There is a barrier so that Landmark 4, and for that matter Landmark 3, cannot be seen from Landmark 1. The course followed is shown by red arrows. Each landmark can be thought of as having a waypoint (e.g., W2), or intermediate step in the whole route, associated with it. (b) Results of the simulation of navigation using spatial view cells implemented in NavSVC.m, the progress of which can be viewed with NavSVC.mp4 (see Supporting information S1). The simulated agent starts at "L1", and then navigates via L2 and L3 to reach the goal at landmark L4. The simulated agent looks for the next landmark, and when the next landmark is being looked at, then moves towards that landmark using taxis, correcting its motion as necessary using error correction to implement the taxis towards the spatial view that is being looked at. When the landmark is reached and the agent is close to it, the agent looks for the next landmark in the list and moves towards it. The direction at which the eyes are looking at the spatial view to guide each leg of the route is shown by the red line. The sequence of landmarks L1–L4 for the spatial view cells is recalled from a sequence memory [Color figure can be viewed at wileyonlinelibrary.com]

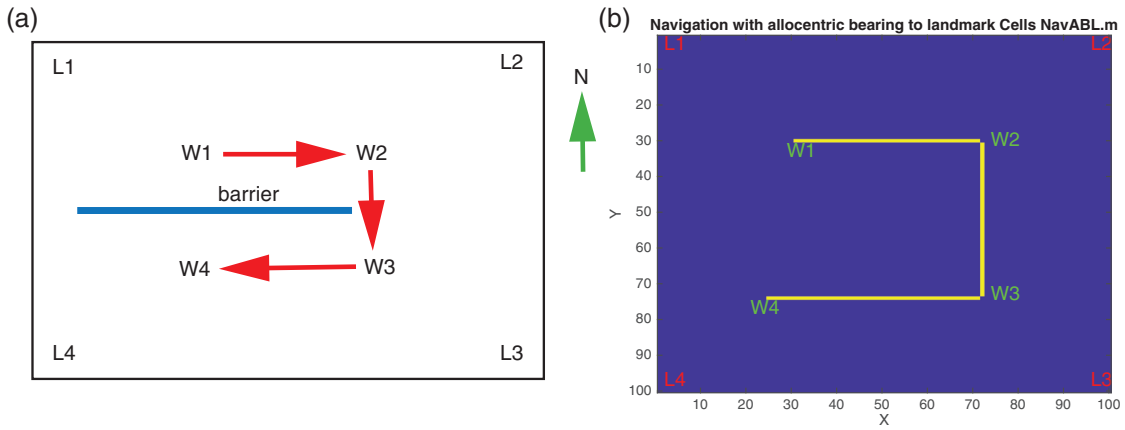

FIGURE 5 (a) An example of navigation using allocentric-bearing-to-a-landmark cells. The task is to start at Waypoint 1 (W1), and to reach Waypoint 4 (W4). There is a barrier so that Waypoint 4, and for that matter Waypoint 3, cannot be seen from Waypoint 1. The course followed is shown by red arrows. The landmarks used are L1-4. North is indicated by N. (b) Results of the simulation of navigation allocentric-bearing-to-a-landmark cells implemented in NavABL.m, the progress of which can be viewed with NavABL.mp4 (see Supporting information S1). The simulated agent starts at Way Point 1 (W1) and then navigates via Way Points 2–3 to reach the goal at Way Point 4. The simulated agent uses head direction cells to determine the direction of navigation, and allocentric-bearing-to-a-landmark cells to determine when a Way Point has been reached. At each Way Point, the agent recalls from a sequence memory (e.g., a continuous attractor network) the next head direction for navigation and the next allocentric-bearing-to-a-landmark to determine whether that Way Point has been reached. An alternative to the use of head direction cells (which are allocentric), is the use of whole body motion cells (which are egocentric) [Color figure can be viewed at wileyonlinelibrary.com]

whole body motion cells; or an allocentric head direction signal to turn to face East; etc.

This navigation could thus be performed using only primate head direction and whole body motion cells. The sequence of steps, and the information associated with each step, could be implemented in the same ways as described for spatial view cells above. Trigonometric calculations are not required, though a Euclidean space is assumed.

This idiothetic navigation (i.e., in the dark or when no view details are available) would be suitable for only a few minutes, for after that time the integration required to compute head direction, and distance travelled based on whole body motion/vestibular inputs becomes inaccurate.

Importantly, this idiothetic type of navigation could be used as a supplement with the strategies described previously using spatial view cells or "allocentric-bearing-to-a-landmark" cells. For example, when navigation using "allocentric-bearing-to-a-landmark cells" described above is being used, it could be helpful to use the known distance between W1 and W2 to help provide information about when W2 has been reached (see Figure 5a). The implementation could use the self-motion cues to update the position in a spatial continuous attractor in the ways described previously (McNaughton et al., 1996; Redish, Elga, & Touretzky, 1996; Rolls & Stringer, 2005; Skaggs, Knierim, Kudrimoti, & McNaughton, 1995; Stringer et al., 2005; Stringer, Rolls, Trappenberg, & Araujo, 2002).

However, a key difference from models of idiothetic navigation in rodents is that in primates the dorsal visual system plays an important role in the idiothetic update of spatial representations, because it takes into account eye position to help compute where the primate is looking in allocentric space (see Figure 3; Rolls, 2020). The transforms and a theory of how they are performed using gain modulation supplemented by a learning rule with a short-term memory trace is summarized in Section 2.6 (Figure 3), with the computational implementation of these coordinate transforms and simulations described elsewhere (Rolls, 2020). The idiothetic updates are for eye position, head direction, and place, and allow representations to be formed that are in allocentric spatial view coordinates. This is useful for primate navigation when visual inputs are not available, for it provides a recall cue to the hippocampal system via the parahippocampal cortex (see Figures 2 and 3) that enables the object at a spatial view location to be recalled even when the spatial view is not visible. That is an important way for identifying the goals for navigation using spatial view cells even when vision is not possible. The implication of this is that much of the idiothetic update for spatial representations and navigation is performed in the primate dorsal visual system (red pathways in Figure 2). This idiothetic update can then communicate with the hippocampal memory system including the parahippocampal gyrus via brain areas such as the retrosplenial cortex and posterior cingulate cortex, as illustrated in Figure 2. The use of the dorsal visual system for idiothetic update of self-motion produced by eye movements as well as by head direction makes this approach to idiothetic update (Rolls, 2020) different from approaches to idiothetic update in rodents, which do not have a fovea and eye movements to fixate locations in the world, and do not have a dorsal visual system with many specializations for foveate vision and the eye movements required, nor spatial view cells to be idiothetically updated by these signals.

4 | METHODS: COMPUTATIONAL MODELS, AND SIMULATIONS TO BE IMPLEMENTED

In this section computational models, and the ways in which the models were simulated, are described. The computational models and

simulations are designed to illustrate the new hypotheses presented in Section 3 about how spatial neurons found in primates including humans could implement navigation.

4.1 | Navigation using spatial view cells

A computational model of a navigational task to illustrate the implementation of navigation by spatial view cells was set up, with the navigational task shown in Figure 4a. A sequence of landmarks is learned and stored, and spatial view cells are used to guide the individual to each landmark in turn by a process of taxis. As described in Section 3, the sequence of landmarks could be stored in human working memory, or in a continuous attractor network, or using hippocampal time cells. The Matlab program NavSVC.m steps through the sequence of landmarks that guide each leg of the route. For each leg of the route (e.g., from Landmark 1 to 2), the individual moves towards the landmark for that leg by looking for the relevant landmark, in this case L2, and making a small movement in the direction of that landmark. When the agent is within a short distance of that landmark, the next leg in the sequence is initiated, in this case by looking for L3, and making small movements towards it. This navigational strategy uses spatial view cells, and moves sequentially towards the location represented in the spatial environment by each spatial view cell. No other neuron types of the type described above are needed, though body turn information implemented by whole body motion cells, or allocentric direction information implemented by head direction cells, could be associated with each landmark to help the individual look for the next landmark in the sequence, as indicated in the program. The details of the methods used in the implementation are provided in the Matlab program NavSVC.m, with some details next.

(The taxis is implemented as follows in the program NavSVC.m. First the individual uses spatial view cells to locate and look at the next landmark. Then the individual moves forwards, and corrects its direction of movement towards the landmark using error correction between the spatial view direction (which is the desired navigational direction), and the actual navigational direction. The direction of the next landmark represented by the direction in which the spatial view cells are firing is calculated for computational convenience in the program by a bearing, but in real life most individuals would implement such a taxis by looking directly at the location that made the relevant spatial view cell fire, facing in that direction, and moving in the direction in which the individual was facing. For example, the individual could rotate its head direction to the angle that made the spatial view cell for the next landmark fire maximally with the eyes looking straight ahead, and move in that head direction. The important point is that all that is required for spatial view cell navigation is a simple form of taxis towards the next landmark. Another detail is that because only taxis is involved, the individual can start from anywhere from which the first (or in principle any other) landmark can be seen, and then taxis is performed towards that landmark until it is reached.)

4.2 | Navigation using allocentric-bearing-to-a-landmark cells

A computational model of a navigational task to illustrate the implementation of navigation by allocentric-bearing-to-a-landmark cells was set up, with the navigational task shown in Figure 5a. In this simulation, for each leg of the route (e.g., from Landmark 1 to 2), the sequence generator provides a heading as a compass direction, and a turn to be made when the allocentric bearing to a landmark reaches a particular value. For the leg from L1 to L2, the Heading is East, and the turn to be made at the end of the leg is to South. The agent moves in the compass direction for a leg until the bearing to the landmark is reached and then turns in the new heading direction specified in the sequence generator. This navigational strategy uses allocentric-bearing-to-a-landmark cells and head direction cells to specify the direction in which to locomote and the turns to be made at the end of each leg. The details of the methods used in the implementation are provided in the Matlab program NavABL.m, and are summarized next for convenience. (In more detail for the implementation, for each leg of the route, the head direction for that leg of the route is recalled from the sequence memory, and the individual moves with that heading until the remembered critical allocentric bearing to the landmark for that leg is reached. At that point, the next leg is started with the same process. Each leg thus requires only one head direction and one critical allocentric bearing for a landmark to be recalled from the sequence memory.)

A similar strategy involves replacement of the head direction cells with whole body motion cells, which relate to no turns for navigation during each leg and a body turn at the end of each leg. The program NavABL.m shows the implementation.

4.3 | Navigation using combinations of allocentric-bearing-to-a-landmark cells: Triangulation

Program NavTRI.m shows how combinations of active "allocentric-bearing-to-a-landmark" cells can be used by triangulation to compute the place where the individual is located. Navigation using this type of triangulation is harder to implement in the brain but is practiced by mariners and was simulated as follows for comparison with the methods previously described. Consider the route illustrated in Figure 5a. The environment is implemented as a Euclidean allocentric topological space as envisaged for rodent place cells (O'Keefe & Nadel, 1978) with X and Y coordinates to define each place. To locomote from W1 to W2, the agent in the simulation calculates its place at every small step of the locomotion using combinations of the active "allocentric-bearing-to-a-landmark" cells. It then calculates, using the geometry of a Euclidean space, the (allocentric) compass bearing to W2 using its current X,Y position and its knowledge of the X,Y position of W2, and uses that bearing as the heading and moves in the direction of that heading. Once the place of the waypoint is reached, the sequence generator loads the X,Y coordinates for the next leg and navigation continues. Simulations of navigation using "allocentric-

bearing-to-a-landmark" cells with triangulation are described in the Results using the program NavTRI.m.

5 | RESULTS: SIMULATIONS OF THE COMPUTATIONAL MODELS

Simulations of the models of navigation described in Section 4 are described in this Results section.

5.1 | Navigation using spatial view cells

In this strategy, navigation is implemented by proceeding via a series of landmarks, to which spatial view cells respond. The navigational task simulated using spatial view cells is illustrated in Figure 4a and was implemented with program NavSVC.m. The simulation worked to perform navigation using spatial view cell information as illustrated in Figure 4b, and this can be viewed as a video by running NavSVC.mp4. The results of the simulation can also be seen by running program NavSVC.m, which allows the start point to be altered, and the details of the implementation to be seen. In the program NavSVC.m, for each leg or node of the route, the navigator looks for the relevant landmark for that leg with spatial view cells, and moves towards the direction specified by the spatial view using error correction of the Navigational Direction ("NavDir") by the spatial view direction of the landmark. When the individual is very close to the landmark, the next leg starts.

5.2 | Navigation using "allocentric-bearing-to-a-landmark" cells

An example of a navigational task performed with "allocentric-bearing-to-a-landmark" cells is illustrated in Figure 5a, and the results of the simulation are shown in Figure 5b, which can be viewed as a video by running NavABL.mp4. The results of the simulation can also be seen by running program NavABL.m, which allows the start point to be altered, and the details of the implementation to be seen.

5.3 | Navigation using combinations of allocentric-bearing-to-a-landmark cells: Triangulation

The navigational task used to illustrate this navigational strategy by triangulation uses the route illustrated in Figure 5 and described in Section 4.3. Places in this Euclidean space are defined by their X,Y coordinates, and this type of geometry is not needed in the strategies described previously. The task is to navigate from an X,Y start place "Start" to Waypoint 1 (W1), and then via the places specified by W2, and W3 to reach the goal at W4. The results for this type of navigation are illustrated in Figure 6, the corresponding video is NavTRI.mp4, and program is NavTRI.m.

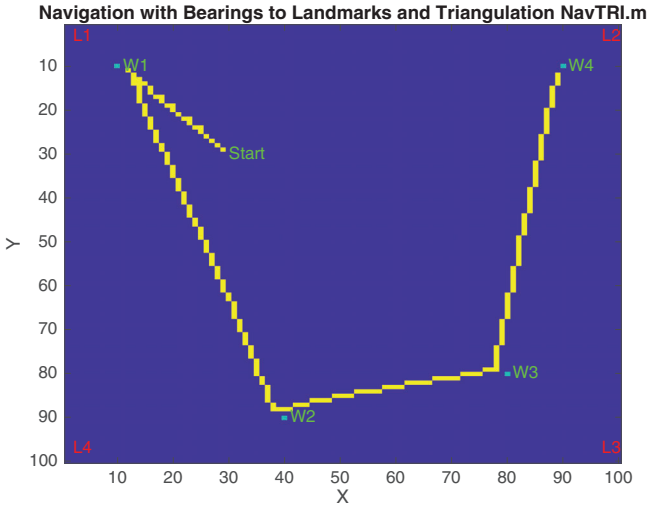

FIGURE 6 Simulation of navigation with triangulation and waypoints. Each place is defined by its X,Y coordinates in a Euclidean space. The task is to start at any X,Y location "Start", and then to navigate to the place at Way-Point 4 (W4) via W1, W2, and W3. Bearing to landmarks using "allocentric bearing to landmark" cells are used to triangulate the place of the agent, and then bearings are computed to move the agent towards the next WayPoint. The simulation is implemented in NavTRI.m, and the progress can be viewed with NavTRI.mp4 (see Supporting information S1). The sequence of allocentric Way Point coordinates is recalled from a sequence memory. L1–L4: landmarks 1–4; W1–W4: Waypoints 1–4 [Color figure can be viewed at wileyonlinelibrary.com]

The navigation can be completed successfully as shown in Figure 6, but at the cost of requiring a topological map in Euclidean space, and the ability to perform trigonometry.

Instead of using geometrical computation in a Euclidean space of the type implemented using triangulation as implemented in NavTRI.m, it is suggested that in primates including humans, simultaneously active spatial view cells for different landmarks in a scene can be associated together to form a spatial representation of a scene, seen from a particular place. As a primate traverses through different places and the scene defined by the landmarks gradually changes, storage of a few such scenes (using for example, the hippocampus to store such episodic memories) could enable later recall of the place, given the set of spatial view cells that are active by comparison with the stored representations. It is proposed that such a neural mechanism might enable spatial view cells to contribute to the lookup in an association memory of a place where the individual is located. This is proposed as another biologically plausible way for spatial view cells to be involved in navigation, by using the viewed scene to recall a place. Such a mechanism might operate to provide useful accuracy even without the need to store too many scenes. Although allocentric-bearing-to-a-landmark cells (which might also encode distance) might be used in addition to or as an alternative to spatial view cells, there is the considerable disadvantage that very many allocentric-

bearing-to-a-landmark cells could be required, as a number of bearings need to be specifiable for each landmark.

6 | DISCUSSION

The approach taken here to navigation in primates (including humans) that makes use of the visual spatial cells found in primates offers relatively straightforward approaches to navigation compared to topological maps based on place cells. The greater complexity of place cell based topological maps has been noted above, and is considered further below. The first approach described here, using spatial view cells, seems very plausible for human navigation, with an example: "Walk towards the church, then walk to the park gate, then walk to the College that you see in front of you." This has some advantages over navigation with "allocentric-bearing-to-a-landmark" cells, in that one need not even know the change of direction for the next waypoint: when one is at one waypoint, one can just look in all directions until the next waypoint is identified with spatial view cells. The reason that this works with spatial view cells is that they respond to a given part of a scene independently of the particular place at which one is located, or the bearing to the landmark (Georges-François et al., 1999). Head direction and whole body turn cells are not essential for but can be used for this type of navigation, to help find the next spatial view at a Waypoint. The utility of landmark-based navigation has been discussed before (Bachiller, Bustos, & Manso, 2008; Ekstrom & Isham, 2017; Erdem & Hasselmo, 2012; Franzius, Sprekeler, & Wiskott, 2007; Kubie & Fenton, 2012; Trullier et al., 1997), but here it is proposed for the first time that spatial view cells could be a key part of the implementation in primates including humans. One interesting property of this type of navigation is that it does not require a representation of place, including the place where the individual is located, or of geometric computations performed in topological maps as is made clear here, and as has been noted previously (Trullier et al., 1997). Indeed, the approach to a landmark requires just taxis, orienting to and moving towards a landmark, as is made clear here and elsewhere (Trullier et al., 1997). This makes navigation using a sequence of spatial view cells a simple and biologically attractive mechanism for navigation on humans, who of course have a number of different strategies that can be used. Spatial view cells could be used in many ways in navigation, but in the simple form in which a taxis is used without a topological map, another mechanism with a map is needed if shortcuts are to be implemented in a way other than by seeing beyond the next landmark to a later one in the sequence.

If a scene is viewed from different places, different sets of landmarks may be visible, or more or less prominent, and different sets of spatial view cells may be activated, or the same set may be differentially activated, as described above. Thus the view that is provided may provide some evidence on where one is located, and that could be useful in navigation. That could supplement the type of information available from allocentric-bearing-to-a-landmark cells.

The spatial view cell approach to navigation proposed here has considerable advantages over navigation using "allocentric-bearing-to-a-landmark" cells, which require a sense of allocentric direction to be maintained while the bearings are being made, which becomes difficult because of inaccuracies in the idiothetic update of the sense of direction for more than a few minutes, with reset being required based for example on a dominant landmark, or on the set of currently viewable landmarks. As a list of waypoints defined by spatial view cells does not suffer from this problem of maintaining a sense of direction, and because it does not require topological knowledge in the form of a map, and because of its simplicity as described here for it involves primarily taxis, it is proposed here that navigation using spatial view cells is the most common type of navigational strategy used in humans and other primates.

Spatial view cells are useful not only for navigation. They are also useful for remembering where the objects, rewards, or goals are in a scene, and for recalling the memory correctly even when the scene is viewed from a different location, bearing angle, head direction, and eye position: that is, spatial view cells are invariant with respect to these transforms (Rolls, 2018; Rolls, 2020). And in addition, spatial view cells are useful for imagery. The proposal is that hippocampal spatial view cells are linked together to form a scene representation in a continuous attractor network (Stringer et al., 2005), and this representation ensures that the parts of the scene are conjoined in the correct spatial order, which is what is also needed for imagery, and also for use in the art of memory (Rolls, 2017). This may be a useful concept to bear in mind by those who believe that episodic memory is viewpoint dependent. Spatial view cells would make a scene maintain its parts in the correct spatial relationship when viewed from many places. It might be more difficult to utilize this type of hippocampal representation to imagine the scene seen from the other side if we have never seen it from the other side before. But for that case, the order would still be present in the hippocampal spatial view continuous attractor, and that could be used to reconstruct in a type of "perspective-taking" what the scene would look like from the other side. This is an interesting way to link human spatial imagery to the representations of scenes "out there" provided in the primate hippocampus by spatial view cells (Rolls, 2018; Rolls, 2021), which are also useful for navigation as described here.

Navigation using the second approach, with "allocentric-bearing-to-a-landmark" cells, is useful when one cannot actually reach one or more of the landmarks because perhaps of some obstacle, but can nevertheless see the landmark and can know the bearing to the landmark from where one is located. The allocentric-bearing-to-a-landmark type of navigation does require a mechanism such as head direction cells to maintain navigation in a stable direction. This type of navigation does need also either whole body motion cells to make the correct rotational turn at a waypoint, or head direction cells to make the correct change of allocentric direction. However, these "allocentric-bearing-to-a-landmark" neurons do provide an alternative to navigation using spatial view neurons if one cannot reach or approach the spatial view part of the scene. The neurons are also of potential importance in the third type of navigation described in Section 4.3 "Navigation using combinations of allocentric-bearing-to-a-landmark cells", in which

triangulation and trigonometry to restitute one's place is used in explicit calculations by humans.

Idiothetic navigation could be implemented in the brain in a number of ways. One is with a 2D continuous attractor network with representations of places, which utilizes body turns at particular parts of the trajectory to implement idiothetic update of place and navigation (Stringer et al., 2002). Another way is with entorhinal cortex grid cells of the type found in rodents, which using head direction and whole body motion / speed may provide a solution (Giocomo, Moser, & Moser, 2011; Hafting, Fyhn, Molden, Moser, & Moser, 2005; Kropff & Treves, 2008; Moser et al., 2014; Moser, Moser, & Roudi, 2014). Some of the problems faced by such models have been described (Edvardsen et al., 2020; Rolls, 2021).

The actual implementation of navigation using neurons of the type described here might be in the primate hippocampus and parahippocampal gyrus, or in the parietal cortex areas such as 7a, retrosplenial cortex, and posterior cingulate cortex (see Figure 2). The case has been made that the human hippocampus is not crucial for navigation, for navigation is impaired only in novel environments, for which the formation of some new memories would be required, but not in familiar environments. In more detail, lesions restricted to the hippocampus in humans result only in slight navigation impairments in familiar environments, but rather strongly impair learning or imagining new trajectories (Bohbot & Corkin, 2007; Clark & Maguire, 2016; Maguire, Intraub, & Mullally, 2016; Spiers & Maguire, 2006; Teng & Squire, 1999). In contrast, lesions in regions such as the parietal cortex or the retrosplenial cortex produce strong topographical disorientation in both familiar and new environments (Aguirre & D'Esposito, 1999; Habib & Sirigu, 1987; Kim, Aminoff, Kastner, & Behrmann, 2015; Maguire, 2001; Takahashi, Kawamura, Shiota, Kasahata, & Hirayama, 1997). This suggests that the core navigation processes (which may include transformations from allocentric representations to egocentric motor commands) can be performed independently by neocortical areas outside the hippocampus, though may utilize hippocampal information related to recent memories (Ekstrom, Arnold, & Iaria, 2014; Miller et al., 2013). In any case, the primate hippocampus can at least contribute to navigation, because of its functions in episodic memory (Feng, Rolls, Cheng, & Feng, 2020; Kesner & Rolls, 2015; Rolls, 2018; Rolls, 2021), which can be useful for navigation.

The implementation of the read-out of the sequential information needed for navigation in the ways described here could be performed in a number of ways. If this is the first time the route has been followed in humans, the list of sequential landmarks could be implemented in the hippocampal episodic memory system. The sequence could be stored by using the time-cells generated in the entorhinal-to-hippocampal system (Eichenbaum, 2014; Eichenbaum, 2017; Howard & Eichenbaum, 2015; Macdonald et al., 2011; Rolls & Mills, 2019; Salz et al., 2016), and associating each landmark with a different time in the time-cell system in the hippocampus. Another possibility is that it is implemented by a continuous attractor network, of the type that has already been described for idiothetic update and thereby navigation using place cells (Stringer et al., 2002) and spatial view cells (Rolls & Stringer, 2005; Stringer et al., 2005). In a continuous attractor network the synaptic connections are strengthened between neurons that are nearby in the space, because they have coactive firing due to the approximately Gaussian shape of their overlapping spatial fields. This sets up a continuous map of space in which adjacent points in the space are joined by their learned coactive firing due to their nearness in the viewed space, as shown for spatial view cells (de Araujo, Rolls, & Stringer, 2001; Rolls, 2016a; Rolls & Stringer, 2005; Stringer et al., 2005). This enables the space to be read out continuously and sequentially, as a bubble of neural activity traverses the space (Rolls, 2021). Consistent with this continuous attractor approach to how viewed spatial representations are learned with transform invariance for viewing position (de Araujo et al., 2001; Rolls, 2020), a visual scene can be learned best in humans when its parts are presented with continuous overlap and from different viewpoints (Holmes, Newcombe, & Shipley, 2018). Another possibility is that the sequence of landmarks is stored in short-term / working memory in the prefrontal cortex (Gilbert & Burgess, 2008; Passingham & Wise, 2012). In any of these cases, previously learned different routes could cross even if some of the landmarks were the same, because each route is a different sequence of landmarks. This separation of the next item in the sequence could be facilitated by the whole body motion or compass direction information that could be associated with each leg of each route.

Models of navigation in rodents typically rely on place cells and how places in a Euclidean space of X,Y coordinates can be used as a basis for navigation (Bicanski & Burgess, 2018; Edvardsen et al., 2020; Hartley et al., 2014; O'Keefe & Nadel, 1978). That is in contrast to the hypotheses developed here based on spatial view cells that are associated with the presence of foveate vision (de Araujo et al., 2001). Interestingly, although the spatial representations in primates and rodents are very different, the type of computation performed is quite similar (Rolls, 2021; Rolls & Wirth, 2018). It is of interest that other animals with foveate vision such as birds also use landmarks for navigation, though they may add to this the capability for a sense of direction that is based on environmental cues that are reliable and do not require idiothetic update (Guilford & Biro, 2014; Guilford and de Perera, 2017).

The theory described here makes many predictions, with some examples now provided. One is that spatial view cells will be found in humans and other primates in brain areas implicated in navigation. A second is that the spatial view cells will be active on legs of routes according to their selectivity and which landmark is currently being used for the navigation. A third is that spatial view cells will display idiothetic update when a landmark being used for navigation is temporarily obscured. A fourth is that in brain regions such as the hippocampus, neurons that respond to combinations of spatial view and a body turn or a move to a new head direction will be found. A fifth is that these combination neurons will be especially evident and selective for views from particular places when that is all the testing allows, whereas in an open environment spatial view cells being used for navigation will be much less place selective. A sixth is that if the navigation is performed sideways rather than moving forward, spatial view cells will respond to the spatial view being looked at and used for navigation, and not at the direction in which the individual is facing. A

seventh is that if navigation is being performed for a highly practiced route, spatial view cells may be used less and will be less active, and instead habit-based procedures such as body turns made after distances traversed will be more evident in the brain systems implementing that type of navigation.

Hippocampal spatial view cells are suited to the computations for navigation described here in a way that inferior temporal cortex object and face cells (Rolls, 2012;Rolls, 2016a; Rolls, 2021) are not, with the two types of neuron very different, as described next. First, inferior temporal cortex visual neurons respond to objects and in some cases faces almost independently of where the objects or faces are in space, with receptive fields that in plain environments are approximately 70° in diameter (Rolls et al., 2003; Tovee, Rolls, & Azzopardi, 1994), and do not depend on the location in the viewed environment where the object is located (Rolls et al., 2003). Inferior temporal cortex neurons that respond to a face of a person or to an object (such as a motor car) independently of where the object or face was would not be useful in navigation to a specified location in a fixed environment. In contrast, hippocampal spatial view neurons respond to a location in a scene (Georges-François et al., 1999; Robertson et al., 1998; Rolls et al., 1997; Rolls et al., 1998; Rolls et al., 2005; Rolls & Xiang, 2006). A key difference is that parts of scenes cannot be moved with respect to other parts of scenes without creating a new spatial scene (Rolls, 2016a; Rolls, 2021). Indeed, that is what distinguishes scene from object representations: object representations are invariant with respect to where in the scene the object is located; but scenes are defined by an overlapping set of locations (such as those encoded by spatial view cells) that overlap in a fixed spatial arrangement with respect to each other (Rolls, 2016a; Rolls, 2017; Rolls, 2021; Rolls, Tromans, & Stringer, 2008). For that reason, hippocampal spatial view cells, but not inferior temporal cortex object or face cells, are useful for navigation. Second, hippocampal spatial view cells can be updated in the dark for several minutes by self-motion of for example the eyes, or even the body (Robertson et al., 1998). This is very helpful for navigation using spatial view cells, for even if the view is obscured temporarily or it is dark, the spatial view cells update their responses idiothetically (by self-motion) to respond when their spatial location in the environment is being looked at (though not seen; Robertson et al., 1998), and as pointed out above, this enables spatial view cells to help with navigation for a few minutes when the spatial view is temporarily obscured. In contrast, inferior temporal cortex neurons do not maintain their firing for more than ∼200–300 ms when the view is obscured (Rolls, 2005; Rolls & Tovee, 1994; Rolls, Tovee, & Panzeri, 1999), and in any case do not encode where the object is in space (Rolls et al., 2003), so would not be useful in navigation. Third, the representation of spatial view by hippocampal spatial view neurons is more sparse than the representation of objects by inferior temporal cortex neurons (section C.3.1.3 of Rolls, 2021). The utility of this is that sparse representations are at a premium in a memory system such as the hippocampus in order to increase the number of memories that can be stored; and the representation is less sparse in the inferior temporal visual cortex where the amount of information that can be represented is at a premium as the inferior temporal visual cortex is a perceptual region (Franco, Rolls, Aggelopoulos, & Jerez, 2007; Rolls, 2021). Fourth, some hippocampal spatial view neurons respond to combinations of objects and spatial views (Rolls et al., 2005) and the recall of each from the other (Rolls & Xiang, 2006), and this is how I propose that episodic memory in primates including humans is implemented (Kesner & Rolls, 2015; Rolls, 2010; Rolls, 2013a; Rolls, 2013b; Rolls, 2016b; Rolls, 2018; Rolls, 2021). These neurons are likely also to be important in navigation to find an object at a remembered location. Other spatial view neurons respond to combinations of particular rewards and where they are in a spatial scene (Rolls & Xiang, 2005), and this is how it is proposed that the one-trial memory for where a reward has been seen in allocentric space "out there" is implemented in primates including humans (Kesner & Rolls, 2015; Rolls, 2018; Rolls, 2021). These neurons are likely also to be important in navigation to find a reward at a remembered location. None of this applies to inferior temporal cortex neurons, which compute invariant representations including over spatial location (Rolls, 2012; Rolls, 2021), do not have spatial preferences for where objects are except in crowded scenes for objects close to the fovea (Aggelopoulos & Rolls, 2005), with no evidence that allocentric spatial coordinates are represented by inferior temporal cortex neurons, or that they are involved in one-trial object-allocentric spatial view or reward-allocentric spatial view associations (Rolls, 2012; Rolls, 2021).

The type of navigation based on spatial view cells can be considered as a true navigational strategy (Trullier et al., 1997), because the strategy would include a sequential list of landmarks, with each landmark in the list potentially being associated with for example a body turn or a change of allocentric heading (using head direction cells) to head for example South, to help find the next landmark. Moreover, the navigation can be to a hidden landmark goal, as illustrated in Figure 3. Such a computation could be implemented in a continuous attractor network forming a chart (Battaglia & Treves, 1998) of linked spatial view cells with associated primate egocentric body turn ("whole body motion" cells (O'Mara et al., 1994) or allocentric head direction cells (Robertson et al., 1999) in ways that have been investigated computationally (Rolls et al., 2008; Rolls & Stringer, 2005; Stringer et al., 2005). Moreover, if the landmarks were temporarily obscured, idiothetic update of the spatial view neurons based on self-motion could occur (Robertson et al., 1998) using the gain modulation mechanisms in the dorsal visual system through to the parietal cortex (Rolls, 2020). An alternative to a continuous attractor network for spatial view cell based navigation could be a short-term or working memory system implemented in the prefrontal cortex (Rolls, 2021) to remember the sequence of landmarks, and this could be particularly advantageous for new routes for which a continuous attractor representation has not already been set up by learning. In contrast to the present theories and models, use for navigation of geometric environmental cues, followed by visual cues only close to the goal has been proposed (Gallistel, 1990; Lee & Spelke, 2010), as has the use of beacons though without the theory that spatial view cells are involved or a model (Ekstrom & Isham, 2017).

7 | CONCLUSIONS

In this research, the key concept has been introduced that navigation using visual landmarks in the environment as represented by primate spatial view cells and "allocentric-bearing-to-a-landmark" cells provides straightforward and new approaches to understanding the implementation of navigational strategies in primates including humans. These strategies are much simpler that those that aim to use topological maps of the type believed to be implemented by place cells in rodents. Moreover, the spatial view cells that as shown here appear to be so useful for primate including human navigation have other great advantages too, for they probably implement the memory of where objects, reward, and goals are in allocentric scene space; and these cells in a continuous attractor network may also underlie human spatial imagery. The navigational strategies described here using spatial neurons found in the primate hippocampus and connected brain areas provide a fundamental and new foundation to understanding the neural mechanisms of navigation in primates including humans.

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CONFLICT OF INTEREST

The author declares no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code availability: Programs to illustrate the navigational strategies described here are available as NavSVC.m, NavABL.m and NavTRI.m, and run under Matlab or the GNU freely available software Octave, will be made available on publication at https://www.oxcns/org/publications. Further information about hippocampal spatial view cells, including videos to illustrate their firing during locomotion, and colored firing rate plot versions of the corresponding papers, are also available at https://www.oxcns/org/publications.

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