Speed cells in the primate hippocampus and navigation

Edmund T Rolls

Oxford Centre for Computational Neuroscience, Oxford, UK, and
Department of Computer Science, University of Warwick, Coventry, CV4 7AL, UK

*Corresponding author information:
Professor Edmund T. Rolls, MA, DPhil, DSc, Hon DSc
Department of Computer Science, University of Warwick, Coventry CV4 7AL, UK.
Email: Edmund.Rolls@oxcns.org
URL: https://www.oxcns.org
https://orcid.org/0000-0003-3025-1292

Summary

A population of hippocampal neurons in macaques responds to the speed of whole body motion in discoveries made with Alain Berthoz. Some of these neurons respond to linear motion, and others to axial rotation. Some of these neurons respond to vestibular information, in that they respond to speed when the view of the world is obscured. Other neurons respond to the optic flow that induces a sense of motion. These primate speed neurons probably are involved in the idiothetic (self-motion) update of primate hippocampal neurons that respond to spatial view. It is proposed that these primate hippocampal system spatial view neurons are involved in navigation especially when the view details are obscured. It is also proposed that these spatial view neurons are involved in episodic memory, enabling world-based recall of locations of objects and people in scenes independently of eye position, head direction, or the place where the individual is located, especially when the view details are obscured. Alain Berthoz made major contributions to these collaborative discoveries by bringing his expertise in the analysis of vestibular and related visual systems to this research, which illustrates the value of interdisciplinary collaboration in neuroscience. Further examples of where interdisciplinary collaboration with theoretical physicists to make computational models of hippocampal function has enabled key advances to be made in neuroscience are described. Understanding the brain at different levels of explanation, from neuronal to neuroimaging to computational, benefits from interdisciplinary expertise.

To understand the functions of the primate hippocampus in memory, we started recording from macaque single neurons during object-location memory tasks (Rolls 1991). The objects were images of objects on a video monitor, and the locations were the locations on the video monitor at which the macaque looked. We found that some neurons in the hippocampus and parahippocampal gyrus had spatial view fields: they responded whenever there was a visual stimulus in some but not other positions on the screen, and some conveyed information about whether a particular object had been seen at that location in the scene before (Miyashita et al. 1989; Rolls et al. 1989). We were able to show that the majority of these hippocampal and parahippocampal spatial view neurons have allocentric, world-based, coordinates in that they responded to a given location on the screen independently of the (egocentric) position of the screen relative to the head (Feigenbaum and Rolls 1991). Further, hippocampal and parahippocampal cortex spatial view neurons code for locations in allocentric space that are being fixated, with responses that are relatively independent of head directions, eye position, and the place where the macaque is located, as long as the spatial view field in the world can be fixated (Rolls et al. 1997; Robertson et al. 1998; Rolls et al. 1998; Georges-François et al. 1999; Rolls 2023b, 2023a).

Given the evidence that the place where the individual is located is represented in the rodent hippocampus (O'Keefe and Dostrovsky 1971; O'Keefe 1979; McNaughton et al. 1983), and that the place can be updated by self-motion (termed idiothetic update) (McNaughton et al. 1991; McNaughton et al. 1996), Alain Berthoz with his research interest and expertise in path integration (Israel et al. 1993; Wiener et al. 2011) was interested to measure whether neurons in the primate hippocampus responded in relation to path integration. Alain Berthoz came to Oxford to work with us on this, and brought with him a French robot (Robulab made by Robosoft S.A.), which I was able to program to produce quantitative velocities for angular (0-100°/s) and linear motion forwards or backwards (with a standard value of 0.2 m/s), with velocities of 0°/s and 0 m/s as the baseline. The macaque sat on top of the robot, which moved within a 2x2x2 m cue-controlled test chamber. The whole chamber could also be rotated round the macaque (O'Mara, Rolls, Berthoz and Kesner (1994)).

It was discovered that some of these hippocampal neurons respond to linear motion (with for example some responding to forward motion, and others to backward motion), and others to axial rotation (with some responding to clockwise and others to anticlockwise rotation). Some of these speed neurons respond to vestibular information, in that they respond to speed when the view of the world is obscured. Other hippocampal neurons respond to the optic flow that induces a sense of motion. These hippocampal neurons were termed 'whole-body motion' neurons , but could be termed 'speed' neurons though that term describes less well that the neurons encode whole body motion (O'Mara, Rolls, Berthoz and Kesner (1994)).

Fig. 1i illustrates the activity of a primate hippocampal whole body motion (speed) neuron that increased its firing rate during backward linear translation, and decreased its firing rate during forward linear translation (O'Mara, Rolls, Berthoz and Kesner (1994)).

Fig. 1ii illustrates the activity of a different primate hippocampal whole body motion (speed) neuron that decreased its firing rate during linear translation of the monkey away from wall 3, and that also decreased its firing rate during linear translation of the test chamber (wall 3) away from the macaque, showing that optic flow can influence the activity of some primate hippocampal whole body motion (speed) cells (O'Mara, Rolls, Berthoz and Kesner (1994)).
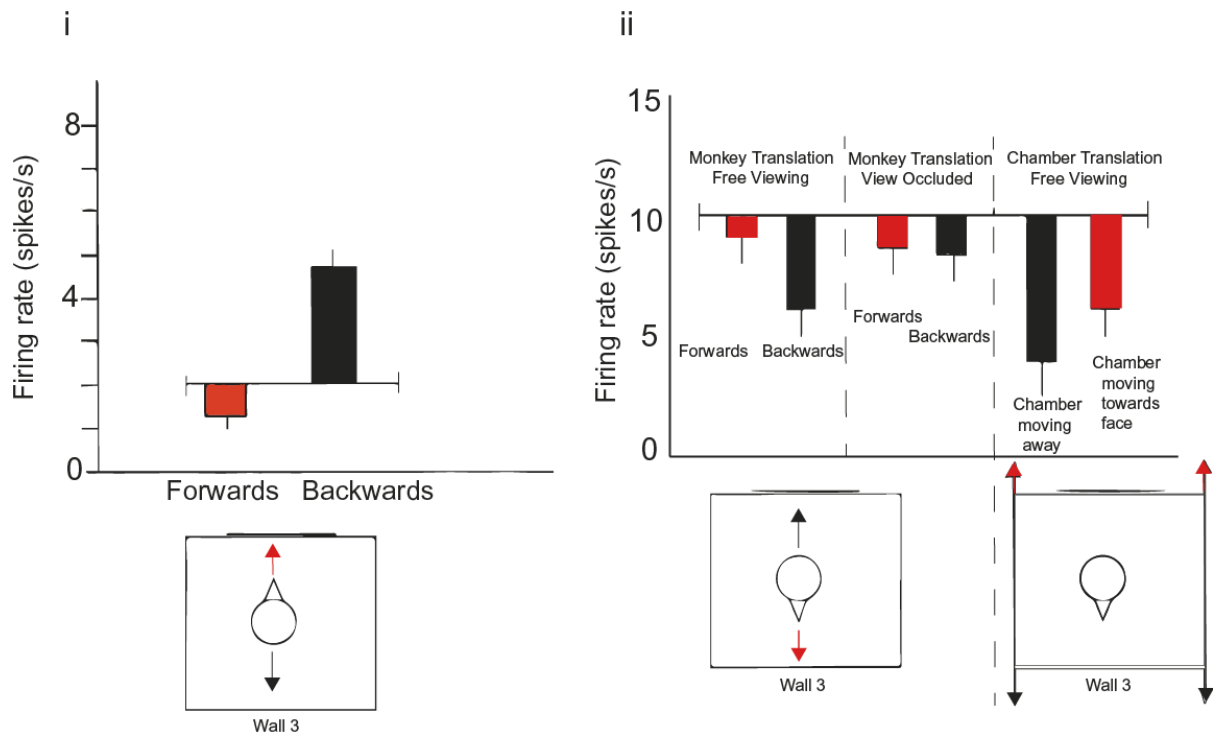
Fig. 1. i. Activity of a primate hippocampal whole body motion (speed) neuron that increased its firing rate during backward linear translation, and decreased its firing rate during forward linear translation.

ii. Activity of another primate hippocampal whole body motion (speed) neuron that decreased its firing rate during linear translation of the monkey away from wall 3, and that decreased its firing rate more during linear translation of the test chamber (with wall 3 being viewed) away from the macaque. The neuron did not respond during linear translation if the view was occluded (middle panel). This neuron was thus activated by visual cues of motion, and not by vestibular cues. (Redrawn from O'Mara, Rolls, Berthoz and Kesner (1994)).

Alain Berthoz made major contributions to these collaborative discoveries (O'Mara, Rolls, Berthoz and Kesner (1994)) by bringing his expertise in vestibular and related visual function, path integration, neuroscience, and engineering to this research. His commitment to careful and controlled measurement using quantitative stimuli was one of the highlights of this collaboration. This commitment is illustrated by the fact that Alain Berthoz brought a French robot from the College de France to Oxford University for this research. Further, this collaboration with Alain Berthoz also draws out the importance of multidisciplinary collaboration in neuroscience, with his expertise in engineering approaches to the vestibular system and path integration fundamental to the success of this research.

The primate speed or whole body motion neurons that we discovered (O'Mara, Rolls, Berthoz and Kesner (1994)) are probably involved in the idiothetic (self-motion) update of primate hippocampal neurons that respond to spatial view (Robertson *et al.* 1998; Rolls 2023a). It is proposed that these primate hippocampal system neurons whole body motion neurons are involved in navigation especially when the view details are obscured. It is also proposed that these neurons are involved in episodic memory, enabling world-based recall of

locations of objects and people in scenes independently of eye position, head direction, or the place where the individual is located, especially when the view details are obscured.

These speed or whole body motion primate hippocampal neurons could also be involved in the idiothetic update of the place where the individual is located, perhaps in addition to the idiothetic update of spatial view. However, in the immediately following research we found that during free open field locomotion in a large laboratory, the majority of macaque hippocampal cells with spatial responses responded to, and encoded information about, the location being viewed, rather than the place where the macaque was located (Rolls *et al.* 1997; Robertson *et al.* 1998; Rolls *et al.* 1998; Georges-François *et al.* 1999). (Some primate place cells were found in a cue-controlled environment (Rolls and O'Mara 1995).) When assessing whether view or place is encoded, it is of course essential to use a factorial design, in which the neuronal responses are compared when the same set of locations are viewed from the same set of places (Rolls 2023b, 2023a). In fact, there is now a revolution in our understanding of the primate including human hippocampus, with evidence now accumulating (Rolls and Wirth 2018, 2023) from different research groups in support of the discoveries (Rolls *et al.* 1989; Feigenbaum and Rolls 1991; Rolls and O'Mara 1995; Rolls *et al.* 1997; Robertson *et al.* 1998; Rolls *et al.* 1998; Georges-François *et al.* 1999) that many primate hippocampal neurons have responses related to where the primate is looking in space (Wirth et al. 2017; Mao et al. 2021; Corrigan et al. 2023; Yang et al. 2023; Piza et al. 2024), with some corresponding evidence in humans (Ekstrom et al. 2003; Miller et al. 2013; Tsitsiklis et al. 2020; Donoghue et al. 2023). Given that path integration for the location in space being viewed (for example in the dark or when the view is obscured (Robertson *et al.* 1998)) must take into account eye position, it is argued that at least part of the path integration for spatial view in primates including humans must be computed in the dorsal visual system (Rolls 2020). There is evidence that in humans the dorsal visual system has connectivity via inferior parietal PGp to the parahippocampal gyrus (Rolls et al. 2022; Rolls 2023a; Rolls et al. 2023a; Rolls et al. 2023b; Rolls 2024), and it is proposed that that pathway is involved in path integration for spatial view cells that involve eye direction position and visual fixation direction (Rolls 2023a), and in helping to build scene representations using eye direction (Rolls 2025). Path integration of primate parahippocampal and hippocampal spatial view cells over place might be more likely to involve hippocampal whole body motion (speed) cells.

Since these discoveries (O'Mara, Rolls, Berthoz and Kesner (1994)), speed cells have now also been described in rodents, in for example the medial entorhinal cortex (Kropff et al. 2015), where they could be used for idiothetic update of place (Giocomo et al. 2011; Moser et al. 2014; Moser et al. 2015). Hippocampal speed (/whole body motion) cells, for angular and translational motion, have also now been confirmed in primates (marmosets) (Piza *et al.* 2024). At least some of these primate speed cells may be interneurons, for some have higher firing rates than is typical of hippocampal pyramidal cells (O'Mara *et al.* 1994; Piza *et al.* 2024).

The research described above on primate whole body motion / speed cells (O'Mara, Rolls, Berthoz and Kesner (1994)) demonstrated the importance of multidisciplinary collaboration, with Alain Berthoz contributing his great expertise in vestibular and related visual function, path integration, and engineering. The importance of multidisciplinary approaches to understanding the operation of brain systems is also exemplified by the computational approach to understanding brain function that was being greatly facilitated by research at the same time on what and how the hippocampus computes that involved Alessandro Treves, a theoretical physicist (Treves and Rolls 1994). An approach that involves what computations

are performed by each brain region, and how they are computed, which can combine multidisciplinary evidence from anatomy, neuronal recording, fMRI activations, effective and functional connectivity, diffusion tractography, the effects of selective brain damage or inactivation, and biologically plausible computational models of brain function and of methods to measure the representation of information by neurons and effective connectivity developed in collaboration with theoretical physicists (Deco and Rolls 2005; Deco et al. 2009; Rolls et al. 2010; Rolls and Treves 2011; Deco et al. 2013; Rolls and Deco 2015; Rolls *et al.* 2022; Rolls *et al.* 2023a; Rolls and Treves 2024; Rolls et al. 2024), is leading to interesting progress in understanding brain function and dysfunction (Rolls 2016a, 2016b, 2021, 2023c, 2023d, 2024; Rolls and Treves 2024; Zhang et al. 2024).

References

Corrigan BW, Gulli RA, Doucet G, Mahmoudian B, Abbass M, Roussy M, Luna R, Sachs AJ, Martinez-Trujillo JC. 2023. View cells in the hippocampus and prefrontal cortex of macaques during virtual navigation. Hippocampus 33:573-585.

Deco G, Rolls ET. 2005. Attention, short-term memory, and action selection: a unifying theory. Prog Neurobiol 76:236-256.

Deco G, Rolls ET, Romo R. 2009. Stochastic dynamics as a principle of brain function. Prog Neurobiol 88:1-16.

Deco G, Rolls ET, Albantakis L, Romo R. 2013. Brain mechanisms for perceptual and reward-related decision-making. Prog Neurobiol 103:194-213.

Donoghue T, Cao R, Han CZ, Holman CM, Brandmeir NJ, Wang S, Jacobs J. 2023. Single neurons in the human medial temporal lobe flexibly shift representations across spatial and memory tasks. Hippocampus 33:600-615.

Ekstrom AD, Kahana MJ, Caplan JB, Fields TA, Isham EA, Newman EL, Fried I. 2003. Cellular networks underlying human spatial navigation. Nature 425:184-188.

Feigenbaum JD, Rolls ET. 1991. Allocentric and egocentric spatial information processing in the hippocampal formation of the behaving primate. Psychobiology 19:21-40.

Georges-François P, Rolls ET, Robertson RG. 1999. Spatial view cells in the primate hippocampus: allocentric view not head direction or eye position or place. Cereb Cortex 9:197-212.

Giocomo LM, Moser MB, Moser EI. 2011. Computational models of grid cells. Neuron 71:589-603.

Israel I, Chapuis N, Glasauer S, Charade O, Berthoz A. 1993. Estimation of passive horizontal linear whole-body displacement in humans. J Neurophysiol 70:1270-1273.

Kropff E, Carmichael JE, Moser MB, Moser EI. 2015. Speed cells in the medial entorhinal cortex. Nature 523:419-424.

Mao D, Avila E, Caziot B, Laurens J, Dickman JD, Angelaki DE. 2021. Spatial modulation of hippocampal activity in freely moving macaques. Neuron 109:3521-3534 e3526.

McNaughton BL, Barnes CA, O'Keefe J. 1983. The contributions of position, direction, and velocity to single unit activity in the hippocampus of freely-moving rats. Exp Brain Res 52:41-49.

McNaughton BL, Chen LL, Markus EJ. 1991. "Dead reckoning", landmark learning, and the sense of direction: a neurophysiological and computational hypothesis. J Cogn Neurosci 3:190-202.

McNaughton BL, Barnes CA, Gerrard JL, Gothard K, Jung MW, Knierim JJ, Kudrimoti H, Qin Y, Skaggs WE, Suster M, Weaver KL. 1996. Deciphering the hippocampal polyglot: the hippocampus as a path integration system. J Exp Biol 199:173-185.

Miller JF, Neufang M, Solway A, Brandt A, Trippel M, Mader I, Hefft S, Merkow M, Polyn SM, Jacobs J, Kahana MJ, Schulze-Bonhage A. 2013. Neural activity in human hippocampal formation reveals the spatial context of retrieved memories. Science 342:1111-1114.

Miyashita Y, Rolls ET, Cahusac PM, Niki H, Feigenbaum JD. 1989. Activity of hippocampal formation neurons in the monkey related to a conditional spatial response task. J Neurophysiol 61:669-678.

Moser EI, Moser MB, Roudi Y. 2014. Network mechanisms of grid cells. Philos Trans R Soc Lond B Biol Sci 369:20120511.

Moser MB, Rowland DC, Moser EI. 2015. Place cells, grid cells, and memory. Cold Spring Harb Perspect Biol 7:a021808.

O'Keefe J, Dostrovsky J. 1971. The hippocampus as a spatial map: preliminary evidence from unit activity in the freely moving rat. Brain Res 34:171-175.

O'Keefe J. 1979. A review of the hippocampal place cells. Prog Neurobiol 13:419-439.

O'Mara SM, Rolls ET, Berthoz A, Kesner RP. 1994. Neurons responding to whole-body motion in the primate hippocampus. J Neurosci 14:6511-6523.

Piza DB, Corrigan BW, Gulli RA, Do Carmo S, Cuello AC, Muller L, Martinez-Trujillo J. 2024. Primacy of vision shapes behavioral strategies and neural substrates of spatial navigation in marmoset hippocampus. Nat Commun 15:4053.

Robertson RG, Rolls ET, Georges-François P. 1998. Spatial view cells in the primate hippocampus: Effects of removal of view details. J Neurophysiol 79:1145-1156.

Rolls ET, Miyashita Y, Cahusac PMB, Kesner RP, Niki H, Feigenbaum J, Bach L. 1989. Hippocampal neurons in the monkey with activity related to the place in which a stimulus is shown. J Neurosci 9:1835-1845.

Rolls ET. 1991. Functions of the primate hippocampus in spatial and non-spatial memory. Hippocampus 1:258-261.

Rolls ET, O'Mara SM. 1995. View-responsive neurons in the primate hippocampal complex. Hippocampus 5:409-424.

Rolls ET, Robertson RG, Georges-François P. 1997. Spatial view cells in the primate hippocampus. Eur J Neurosci 9:1789-1794.

Rolls ET, Treves A, Robertson RG, Georges-François P, Panzeri S. 1998. Information about spatial view in an ensemble of primate hippocampal cells. J Neurophysiol 79:1797-1813.

Rolls ET, Grabenhorst F, Deco G. 2010. Choice, difficulty, and confidence in the brain. Neuroimage 53:694-706.

Rolls ET, Treves A. 2011. The neuronal encoding of information in the brain. Prog Neurobiol 95:448-490.

Rolls ET, Deco G. 2015. Stochastic cortical neurodynamics underlying the memory and cognitive changes in aging. Neurobiol Learn Mem 118:150-161.

Rolls ET. 2016a. Cerebral Cortex: Principles of Operation. Oxford: Oxford University Press.

Rolls ET. 2016b. A non-reward attractor theory of depression. Neurosci Biobehav Rev 68:47-58.

Rolls ET, Wirth S. 2018. Spatial representations in the primate hippocampus, and their functions in memory and navigation. Prog Neurobiol 171:90-113.

Rolls ET. 2020. Spatial coordinate transforms linking the allocentric hippocampal and egocentric parietal primate brain systems for memory, action in space, and navigation. Hippocampus 30:332-353.

Rolls ET. 2021. Brain Computations: What and How. Oxford: Oxford University Press.

Rolls ET, Deco G, Huang CC, Feng J. 2022. The effective connectivity of the human hippocampal memory system. Cereb Cortex 32:3706-3725.

Rolls ET. 2023a. Hippocampal spatial view cells for memory and navigation, and their underlying connectivity in humans. Hippocampus 33:533-572.

Rolls ET. 2023b. Hippocampal spatial view cells, place cells, and concept cells: View representations. Hippocampus 33:667-687.

Rolls ET. 2023c. Brain Computations and Connectivity. Oxford: Oxford University Press, Open Access.

Rolls ET. 2023d. Emotion, motivation, decision-making, the orbitofrontal cortex, anterior cingulate cortex, and the amygdala. Brain Struct Funct 228:1201-1257.

Rolls ET, Deco G, Huang C-C, Feng J. 2023a. Multiple cortical visual streams in humans. Cereb Cortex 33:3319-3349.

Rolls ET, Deco G, Huang CC, Feng J. 2023b. The human posterior parietal cortex: effective connectome, and its relation to function. Cereb Cortex 33:3142-3170.

Rolls ET, Wirth S. 2023. Hippocampal system neurons encoding views in different species: Introduction to the Special Issue of Hippocampus 2023. Hippocampus 33:445-447.

Rolls ET. 2024. Two what, two where, visual cortical streams in humans. Neurosci Biobehav Rev 160:105650.

Rolls ET, Treves A. 2024. A theory of hippocampal function: New developments. Prog Neurobiol 238:102636.

Rolls ET, Yan X, Deco G, Zhang Y, Jousmaki V, Feng J. 2024. A ventromedial visual cortical 'Where' stream to the human hippocampus for spatial scenes revealed with magnetoencephalography. Communications Biology 7:1047.

Rolls ET. 2025. A theory and model of scene representations with hippocampal spatial view cells. Hippocampus 35:e70013.

Treves A, Rolls ET. 1994. A computational analysis of the role of the hippocampus in memory. Hippocampus 4:374-391.

Tsitsiklis M, Miller J, Qasim SE, Inman CS, Gross RE, Willie JT, Smith EH, Sheth SA, Schevon CA, Sperling MR, Sharan A, Stein JM, Jacobs J. 2020. Single-neuron representations of spatial targets in humans. Curr Biol 30:245-253 e244.

Wiener JM, Berthoz A, Wolbers T. 2011. Dissociable cognitive mechanisms underlying human path integration. Exp Brain Res 208:61-71.

Wirth S, Baraduc P, Plante A, Pinede S, Duhamel JR. 2017. Gaze-informed, task-situated representation of space in primate hippocampus during virtual navigation. PLoS Biol 15:e2001045.

Yang C, Chen H, Naya Y. 2023. Allocentric information represented by self-referenced spatial coding in the primate medial temporal lobe. Hippocampus 33:522-532.

Zhang B, Rolls ET, Wang X, Xie C, Cheng W, Feng J. 2024. Roles of the medial and lateral orbitofrontal cortex in major depression and its treatment. Mol Psychiatry 29:914-928.