Learning and Neural Coding in Virtual Reality

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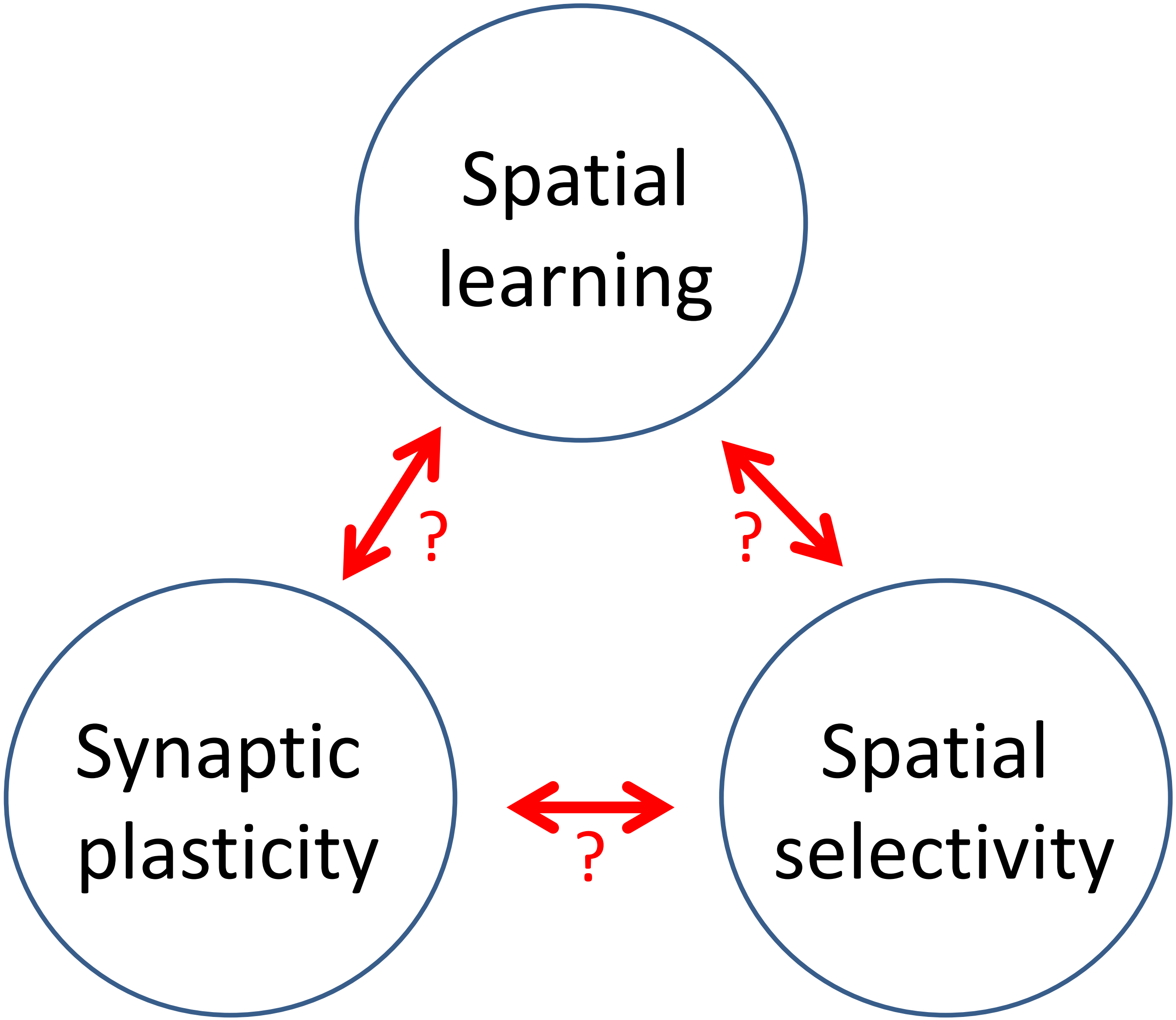
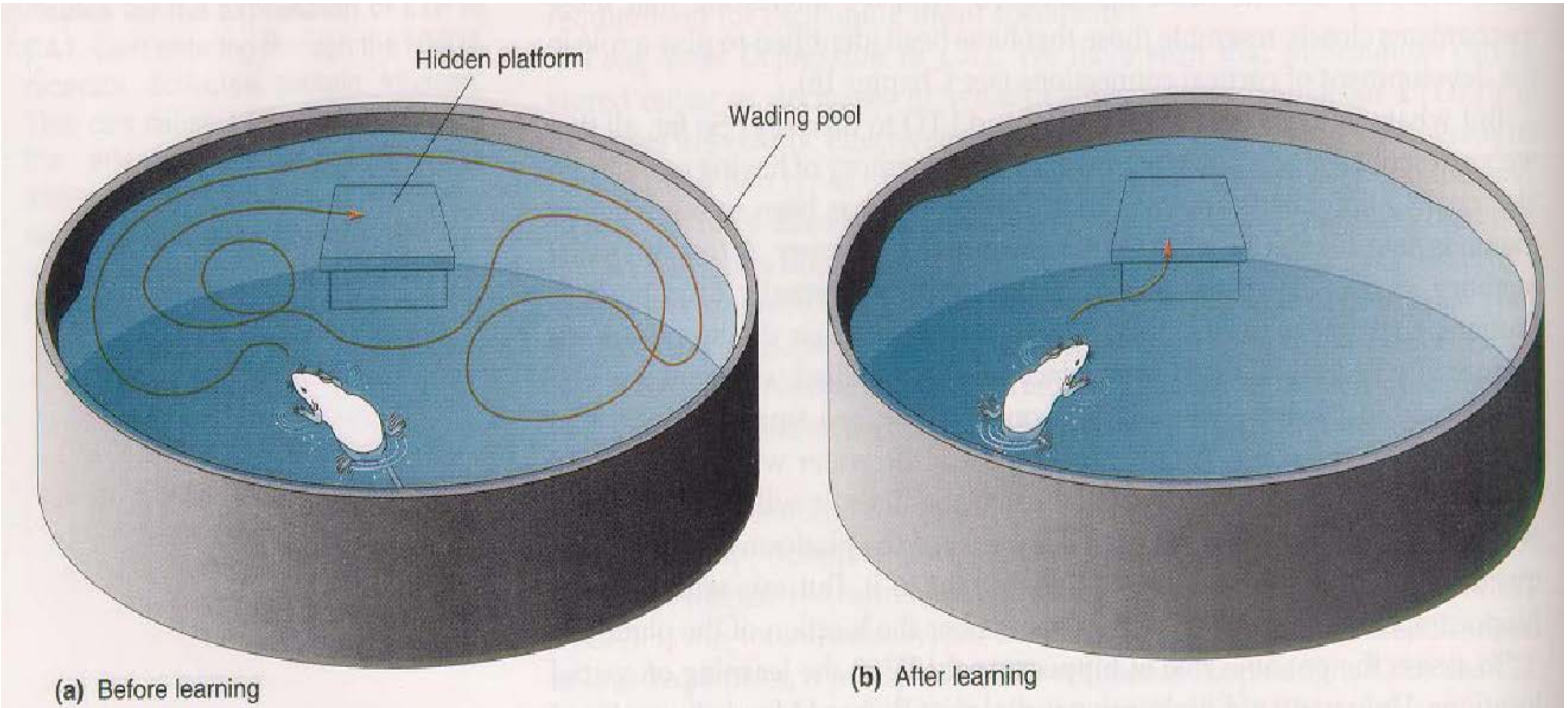
Mechanisms of spatial learning

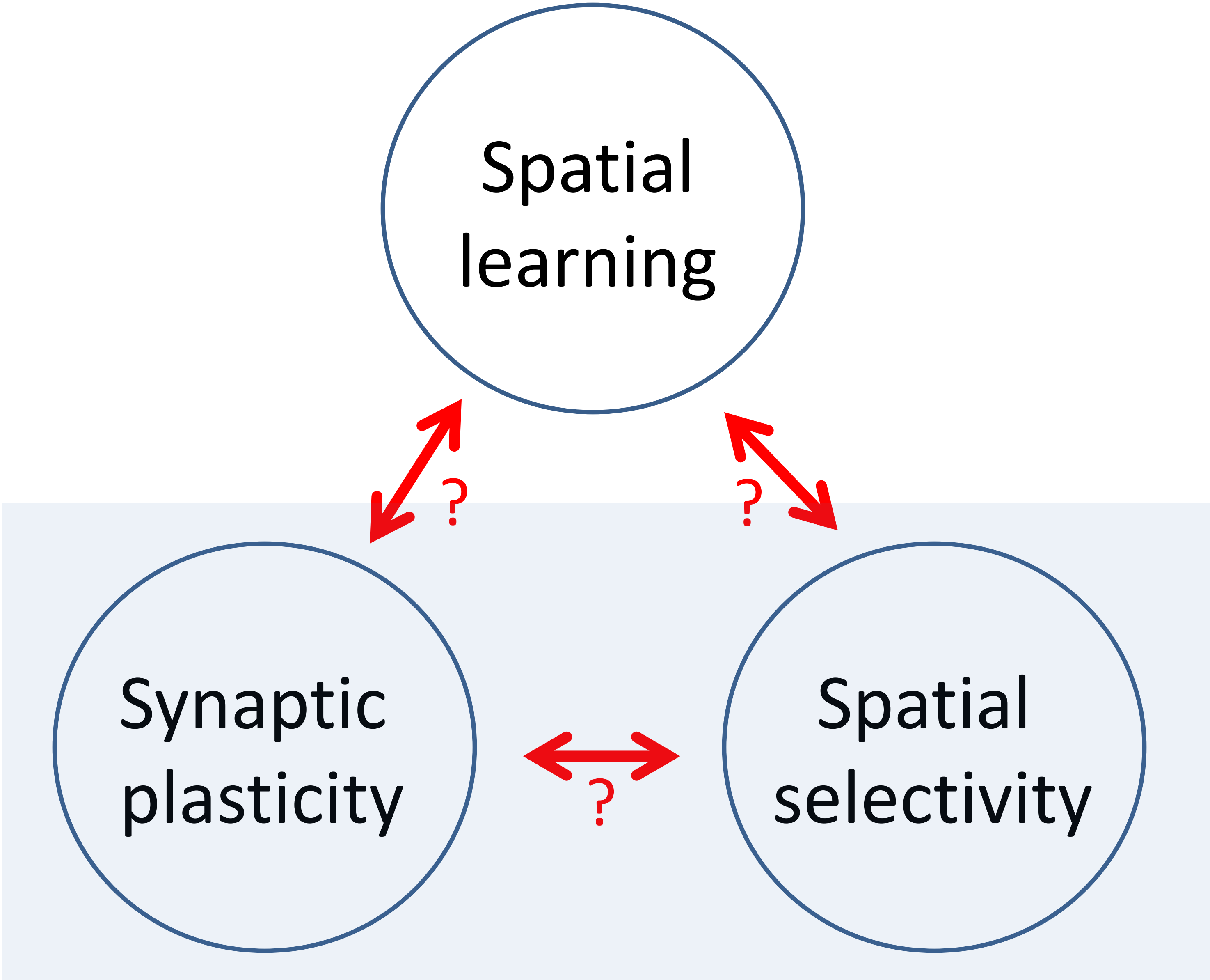


Morris Water Maze test of spatial memory



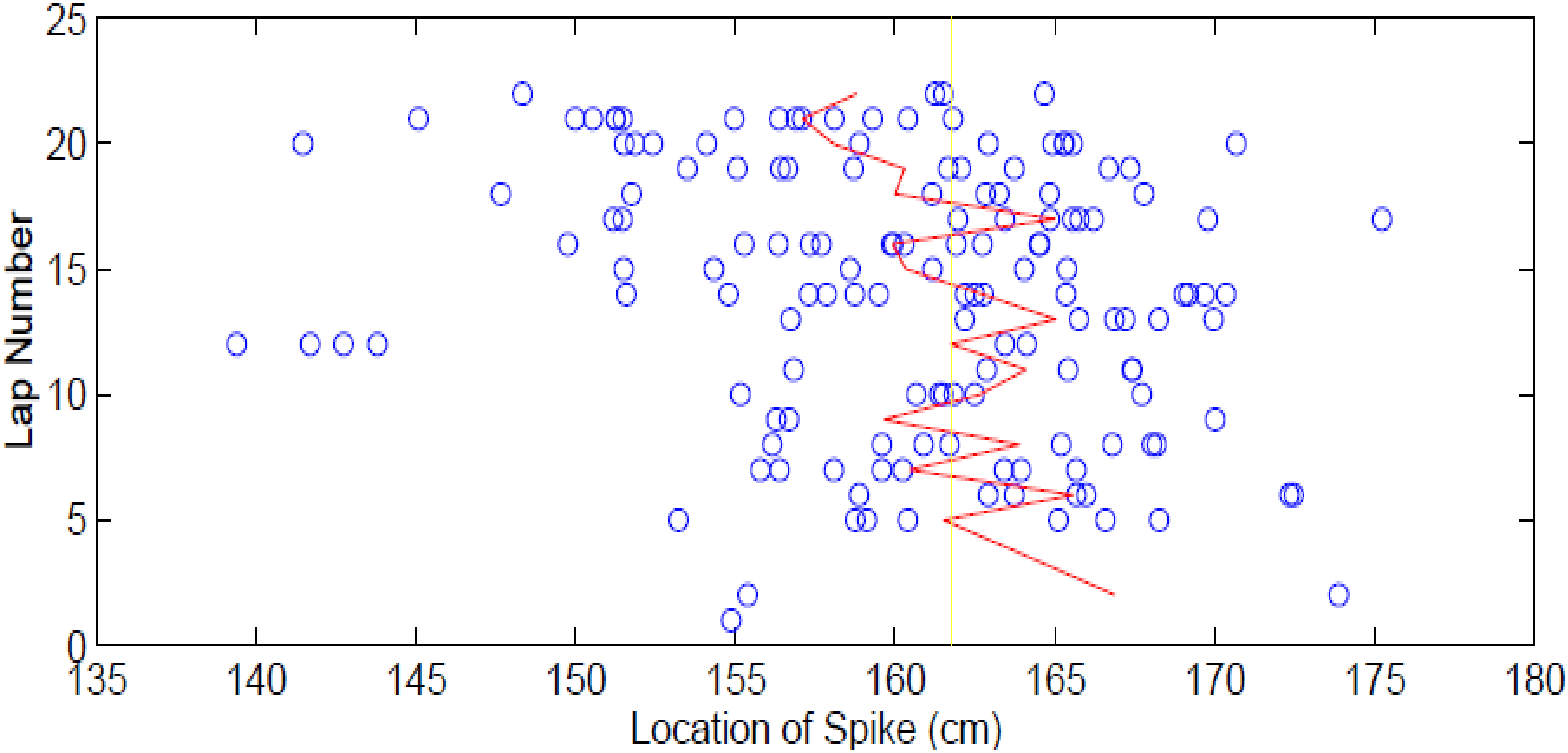
- Distal visual cues provide information about spatial location.
- NMDAR within hippocampus are required for this learning.
- Behavior changes with experience and place cells' activity depends on behavior.

Mechanisms of spatial learning



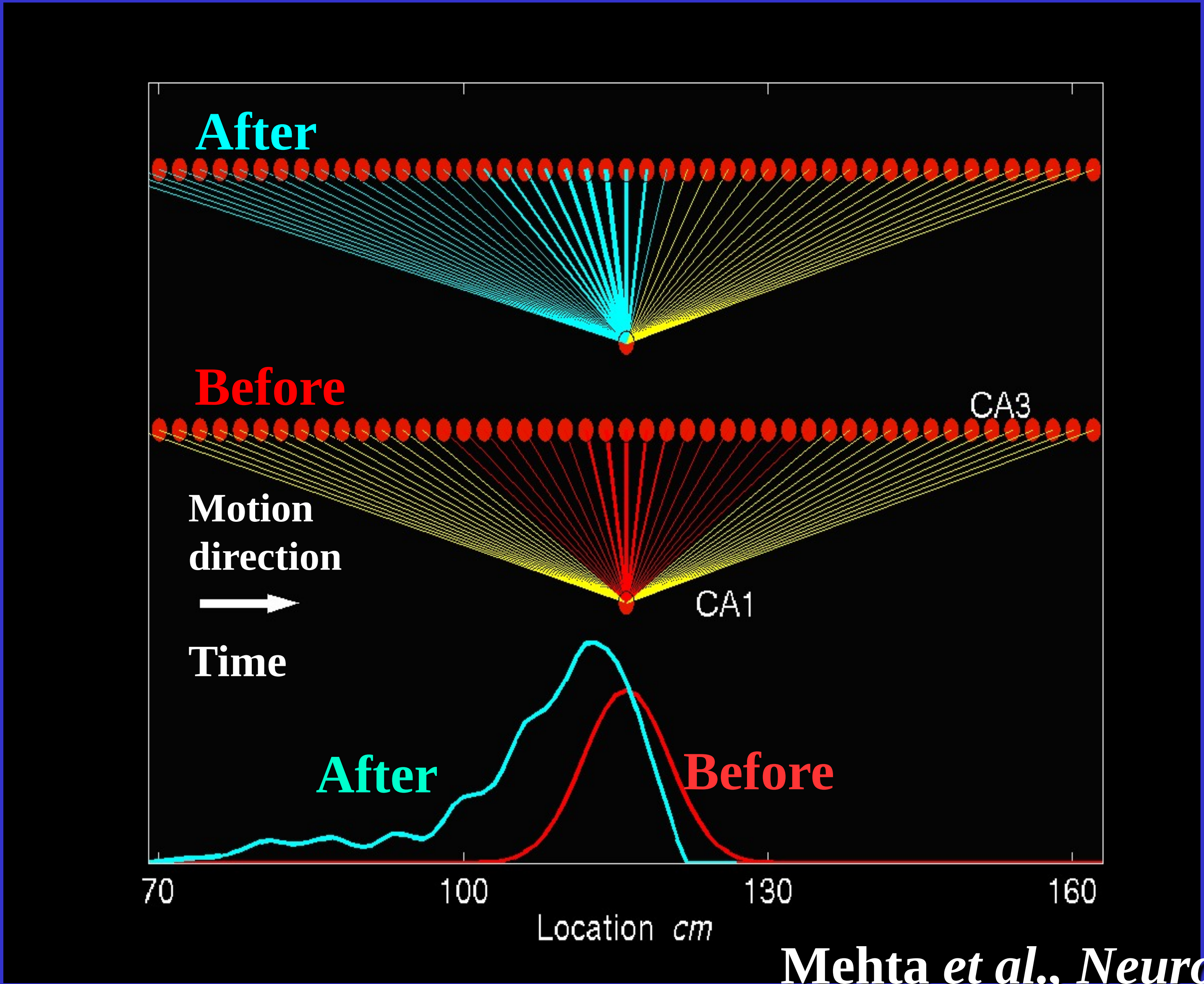
Effect of learning on place cells when neither behavior nor stimuli change

Rapid, experiential changes in place cells' activity



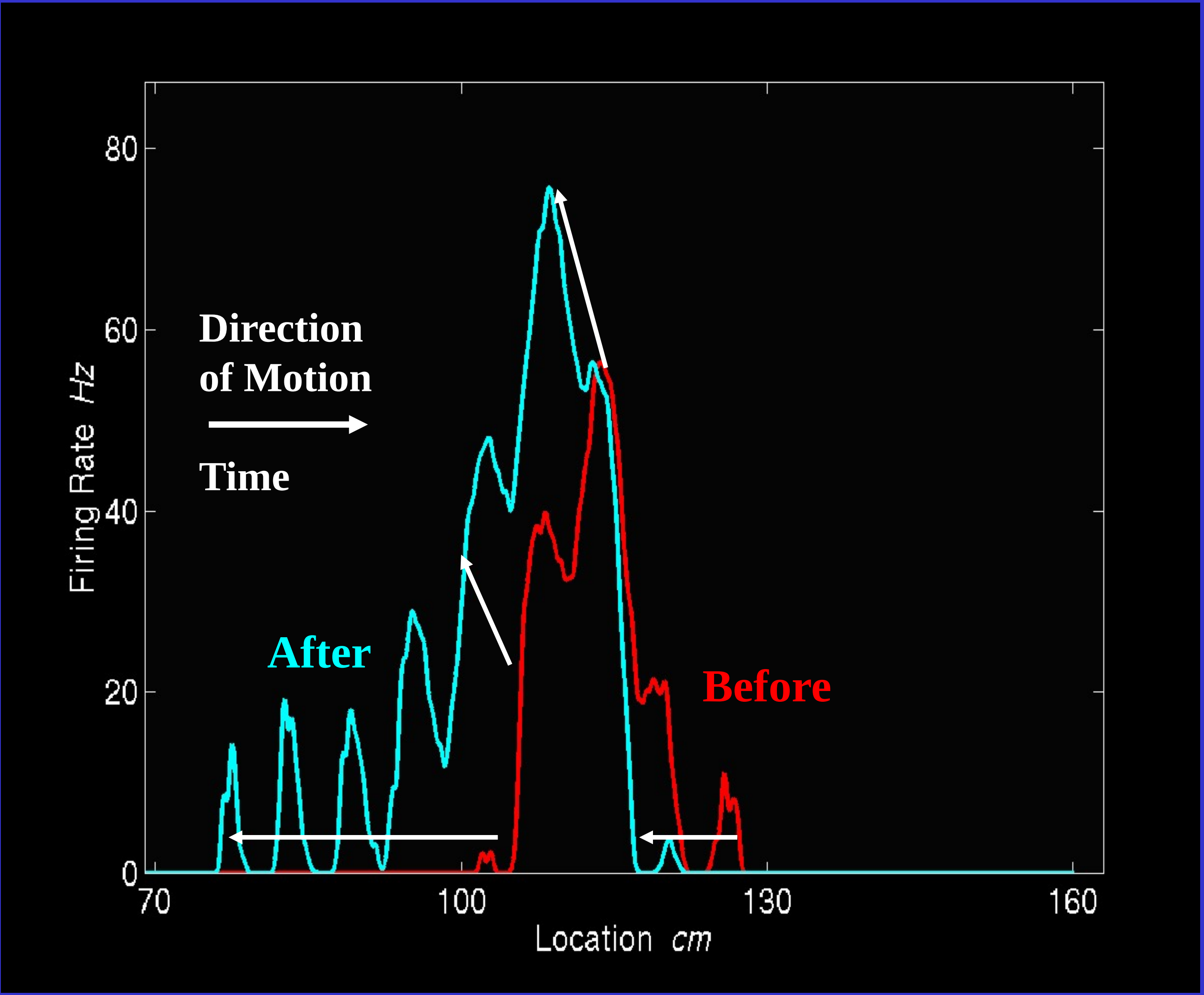
Mehta, McNaughton comp Neuro 1996, PNAS 1998

Computational Model of Effect of STDP on CA1 place cells' activity



Mehta *et al., Neuron 2000*

Predictions of computational models of sequence learning via STDP: Asymmetric place field plasticity



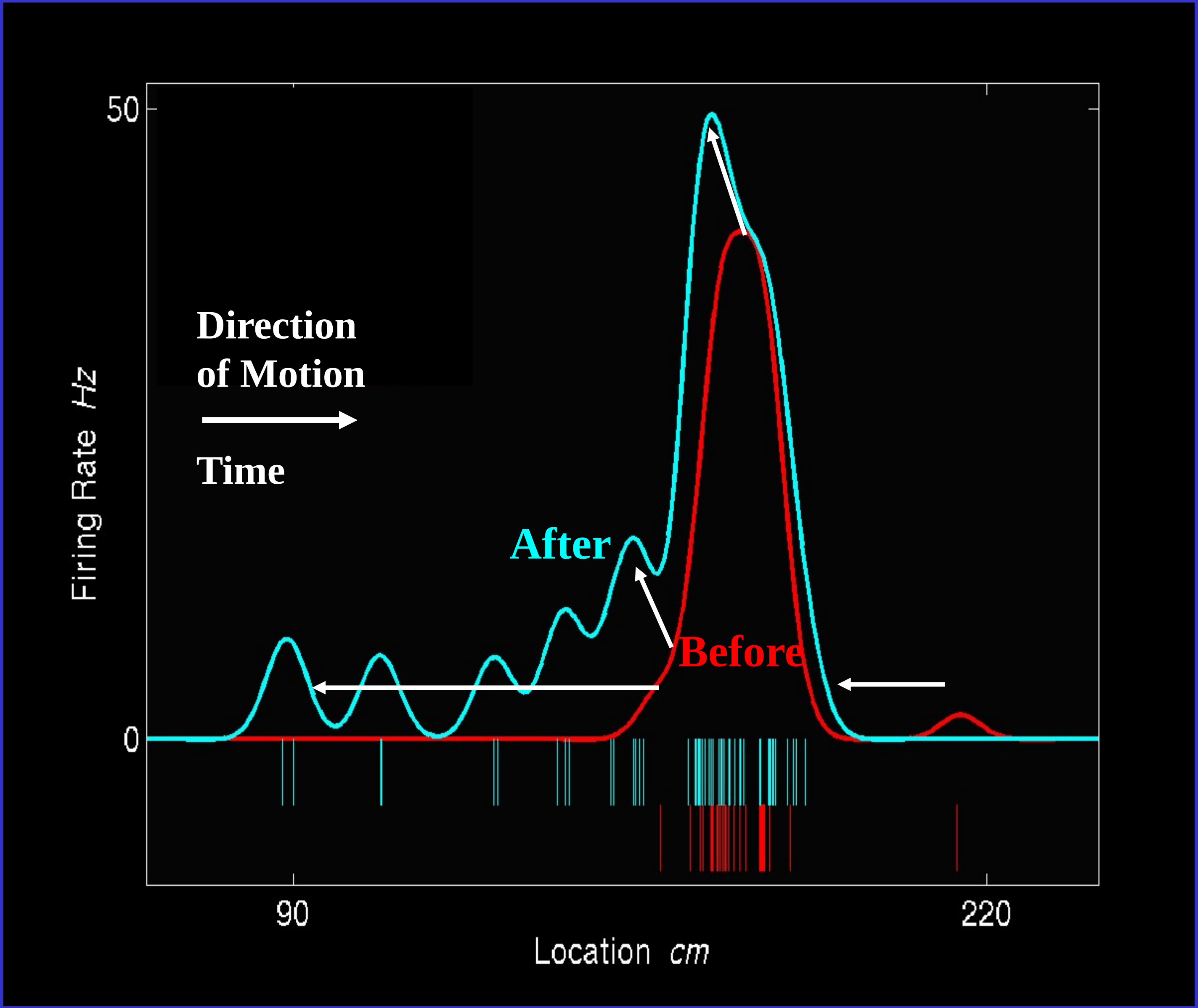
Mehta *et al.*,
Comp Neuro 1996,
Neuron 2000,
Comp Neuro 2001,
Neuroscientist 2001,

Abbott *et al.*,
Cereb. Cortex 1996,
Neural Comp 1996,
J. comp. neuro. 1997,

Hasselmo et al.,
J. Neurophys 1997

***Knierim et al.*,**
Neural comp 2005

Experimental tests of the model: Rapid, experiential, place cell plasticity



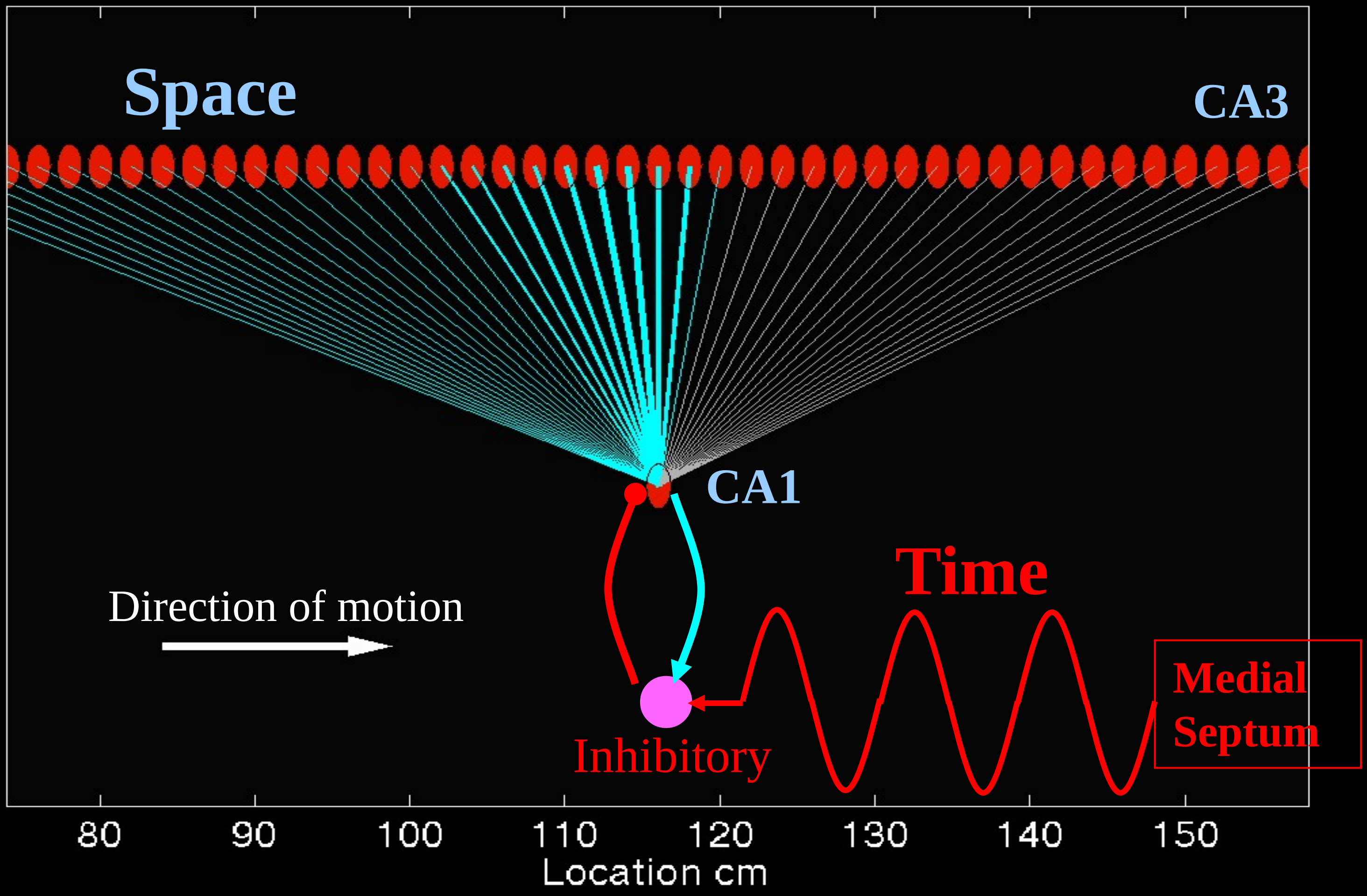
Mehta *et al.*,
Comp Neuro 1996,
PNAS 1997,
Neuron 2000,
Comp Neuro 2001,
Neuroscientist 2001,
Nature 2002

Knierim *et al.*,
Neuron 2004
Neuron 2006

Frank et al.
J. Neuro 2008

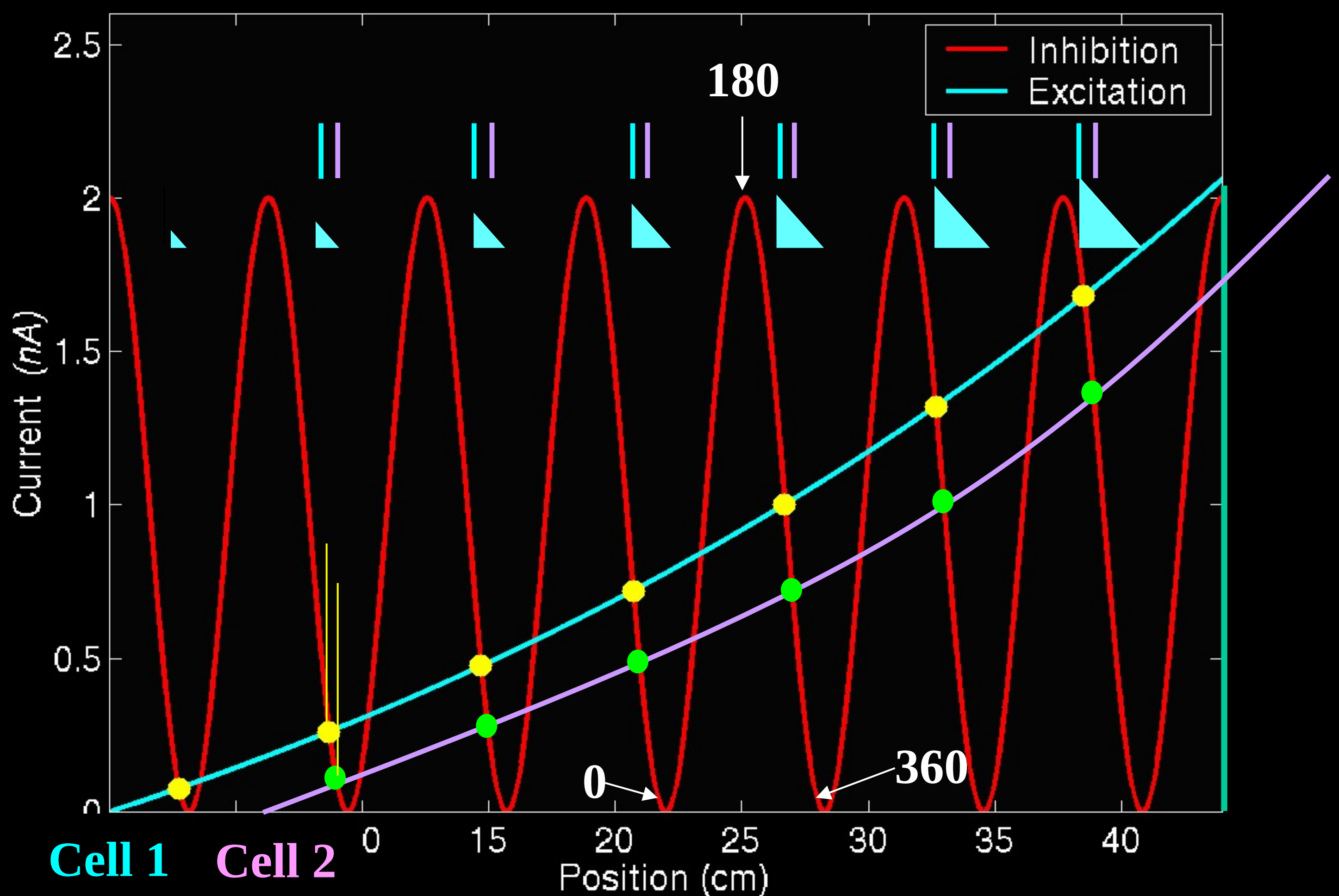
Other brain regions
Merzenich et al.
Y. Dan et al.
M. Poo et al.
Engert et al.

A model for generating a temporal Code from a Rate code



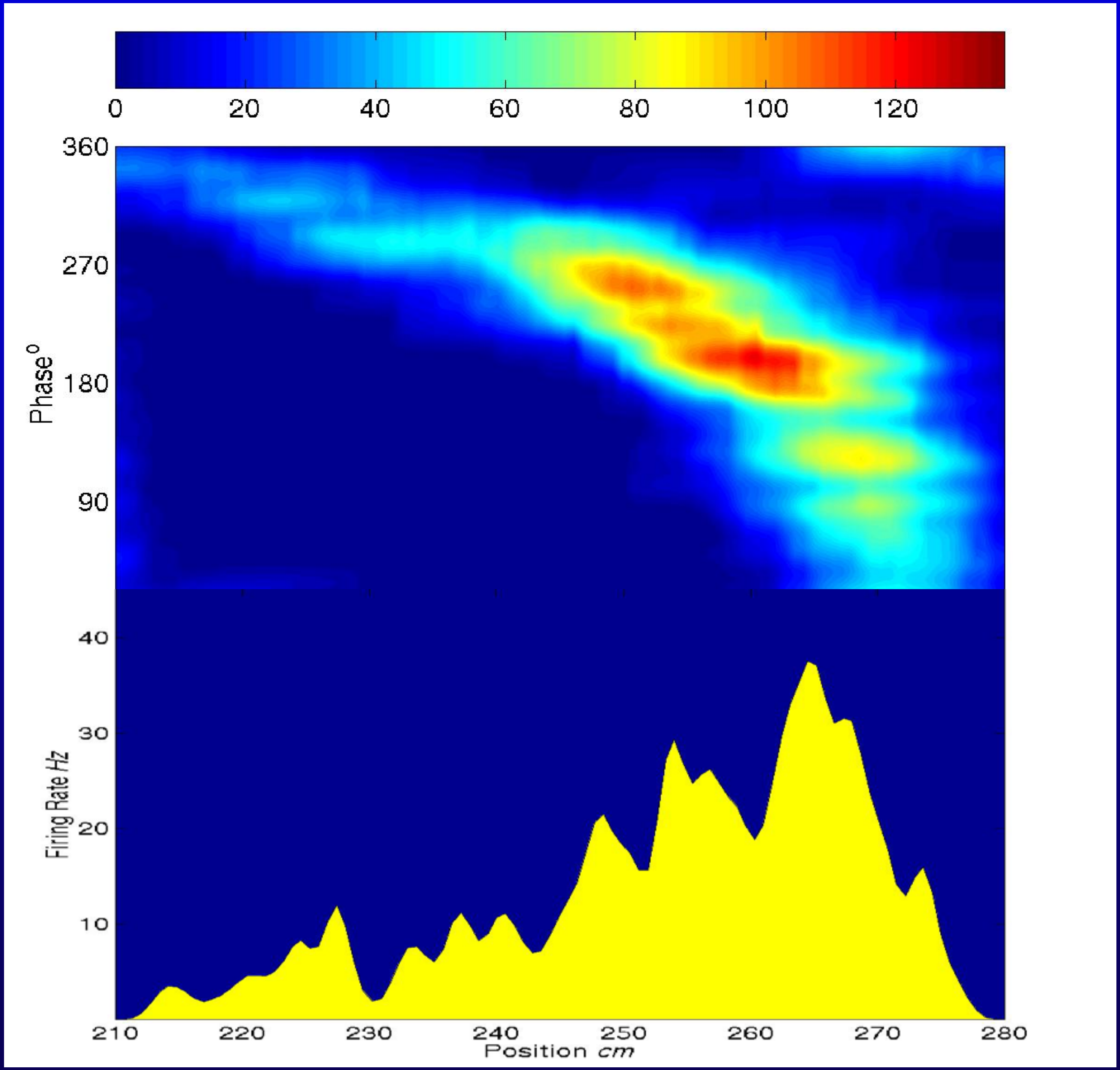
Mehta et al., *Neuroscientist 2001*, *Nature* 2002

A Model of generating a temporal Code: Interaction between asymmetric excitation & oscillations



Mehta et al., *Neuroscientist 2001, Nature* 2002

Experimental evidence for the model

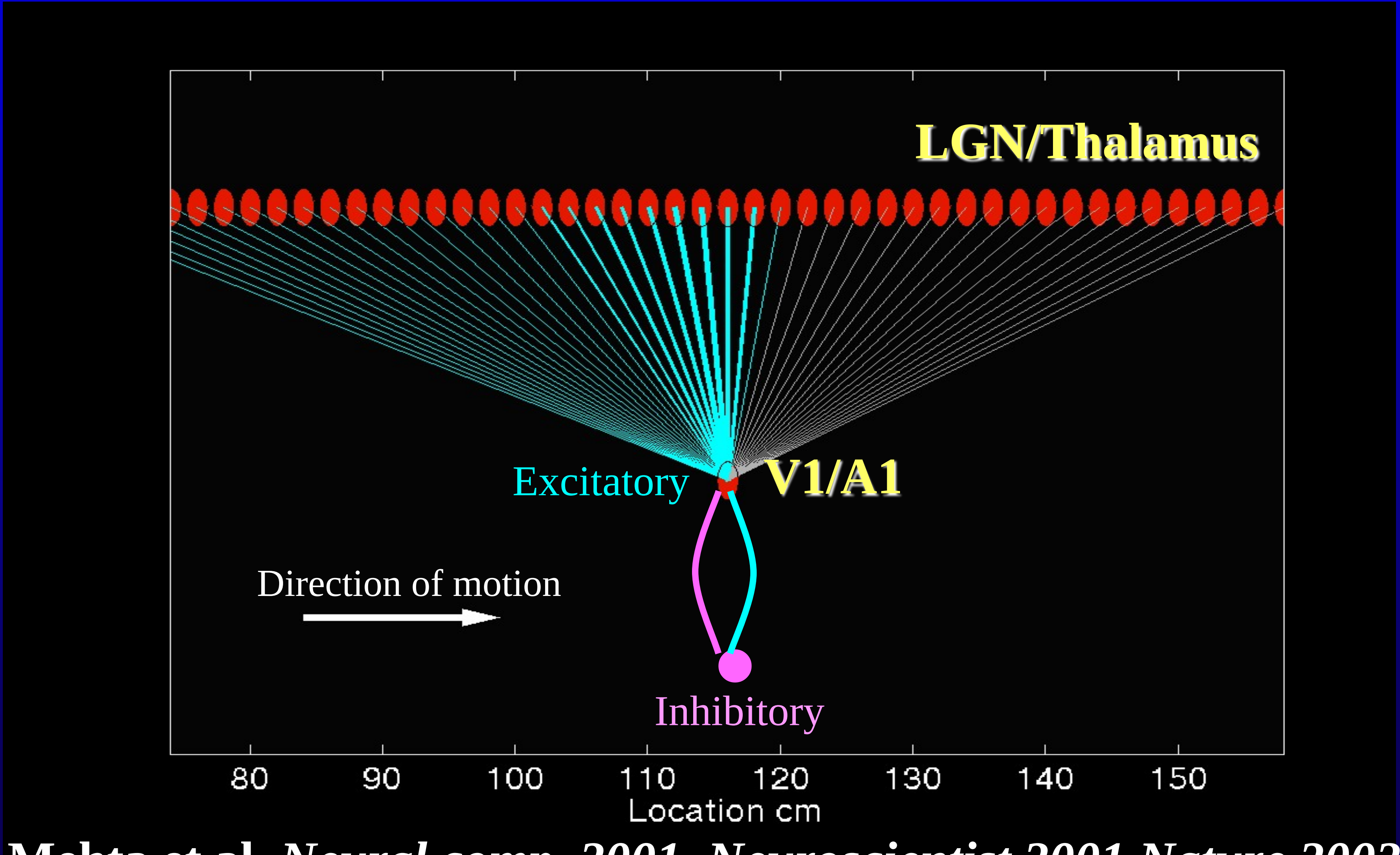


Mehta et al., *Nature* 2002

Place cell plasticity and synaptic plasticity

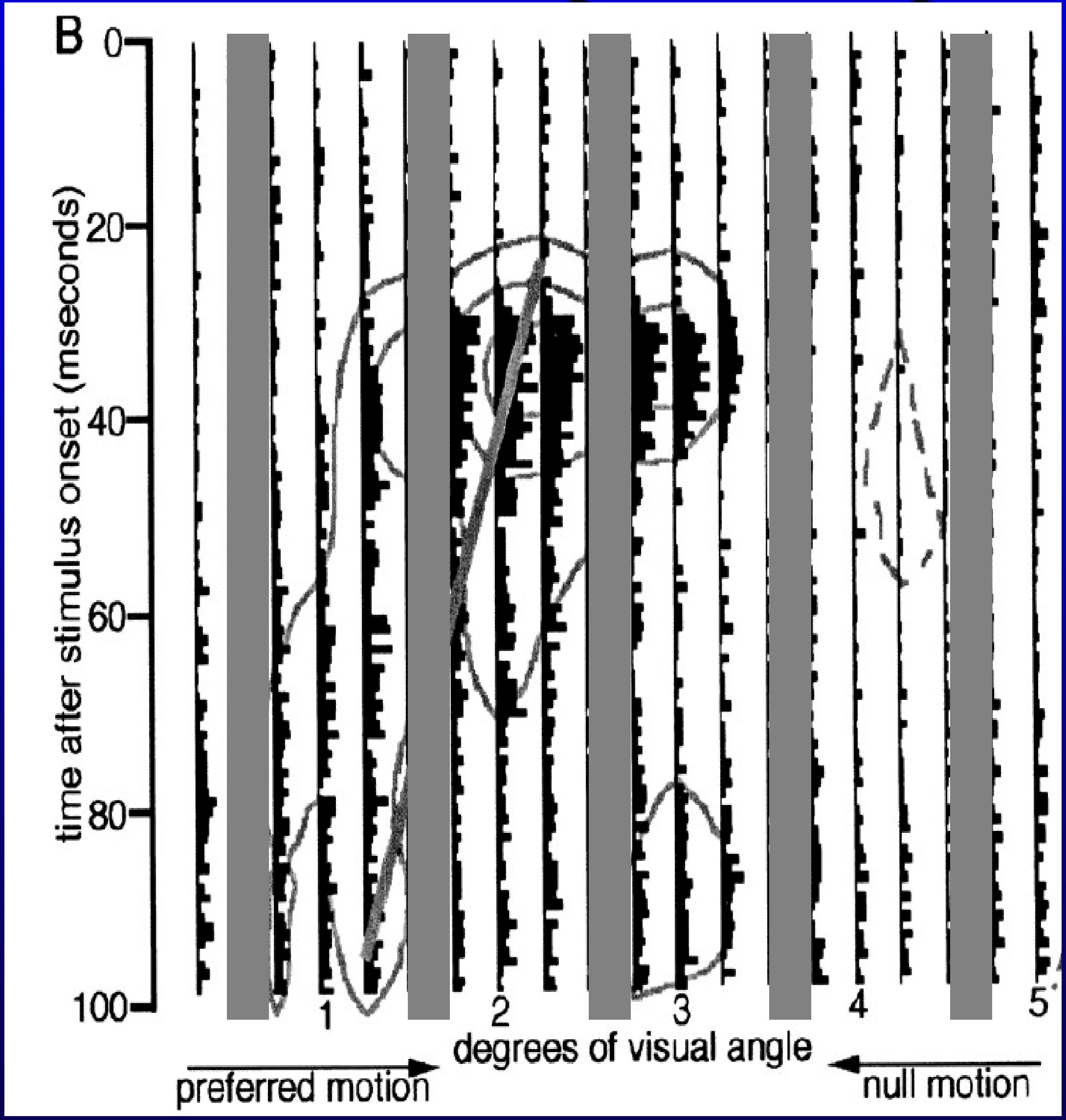
- More than two-fold change in firing rate and the asymmetry of place fields within a couple of minutes.
- Changes are environment and NMDAR-dependent. The results provide an evidence for how STDP can influence receptive fields.
- Anticipatory changes in place cells' activity could allow the animals to predict the future location and learn navigational maps of space.
- Interaction between spatially asymmetric input and periodic inhibition can generate a temporal/phase code:
  - phase as a function of position, nonlinear dependence of phase on position, phase precession independent of hippocampal shutdown, model insensitive to oscillation frequency noise, does not require a unique network connectivity

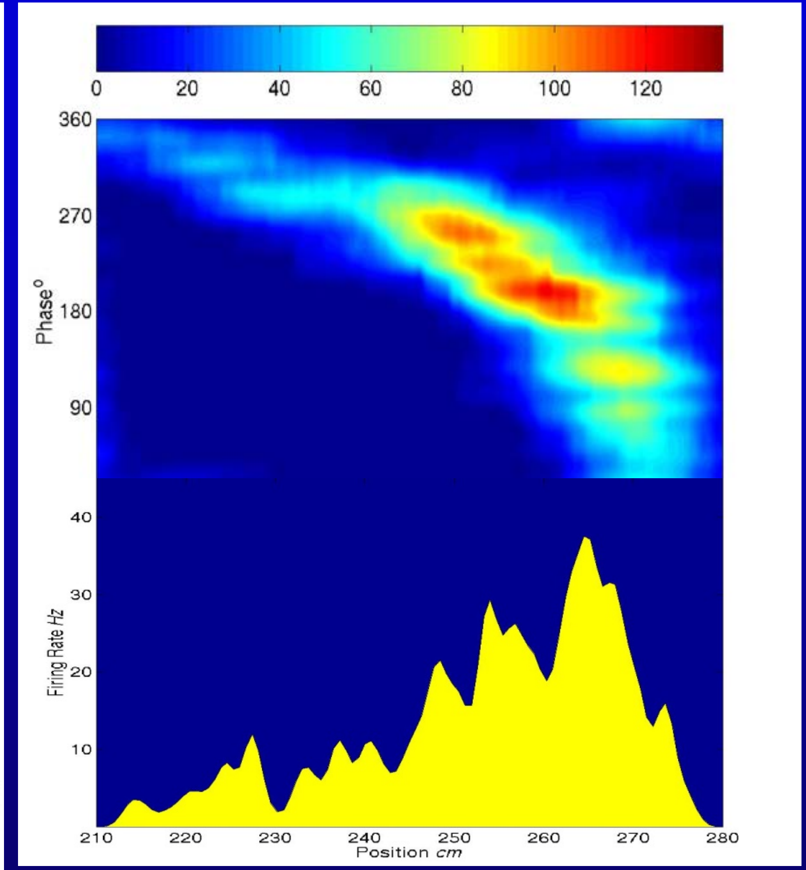
Asymmetric excitation + Delayed inhibition:
Direction Selectivity, inseparable STRF in V1



Mehta et al. *Neural comp. 2001, Neuroscientist 2001 Nature 2002*

Direction selective cells of hippocampus and V1 have a similar spatio-temporal structure!



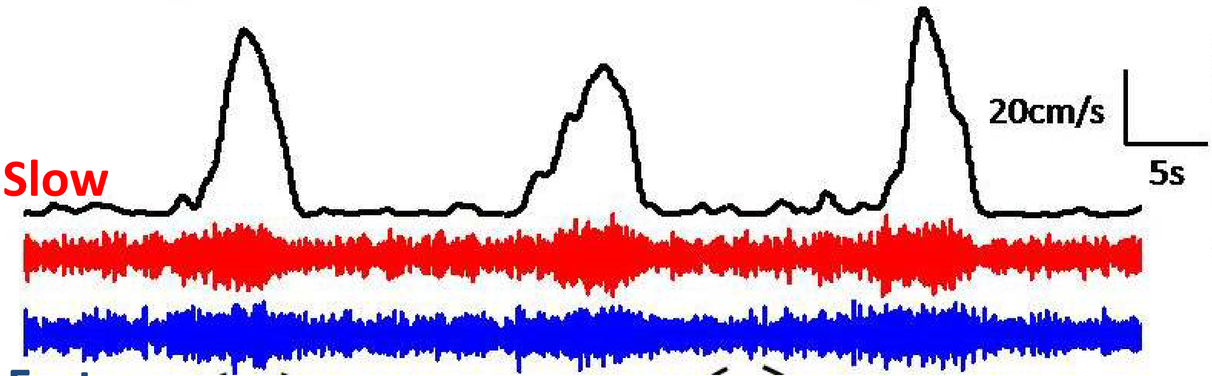


Mehta et al., *Neurocomp* 2000

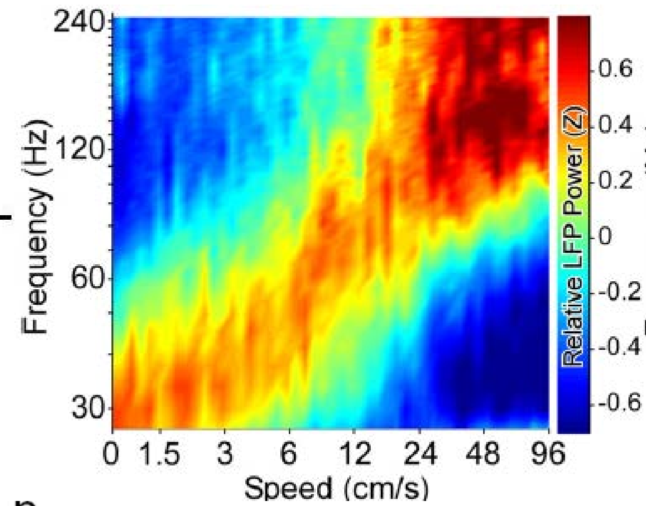
(Livingstone, *Neuron* 1998)

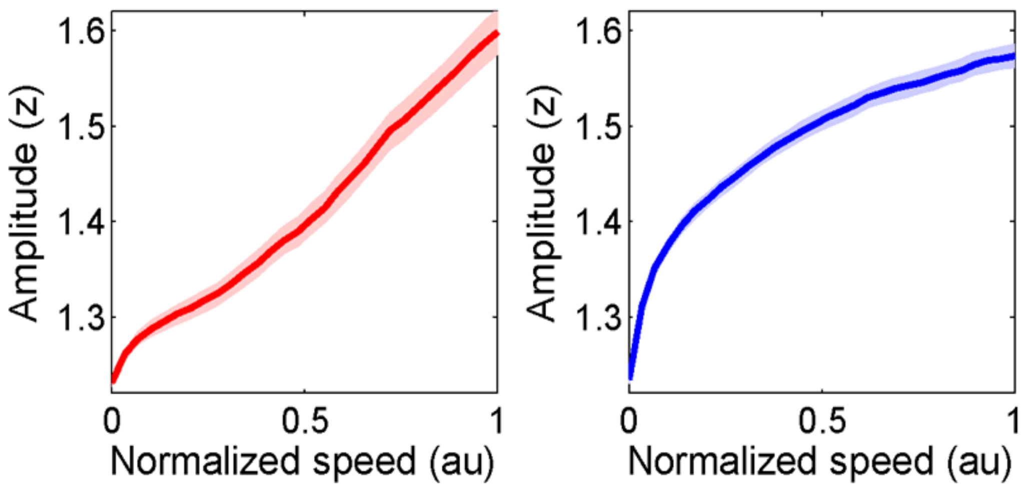
Speed modulates CA1 gamma amplitude, frequency and theta-phase

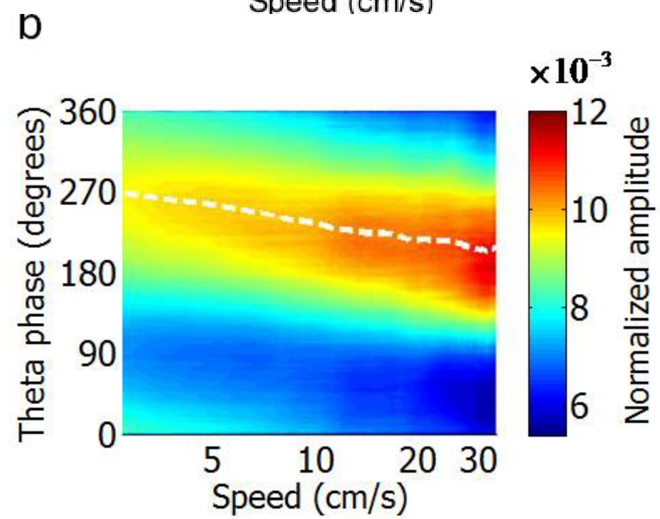
ɣ Slow



ɣ Fast



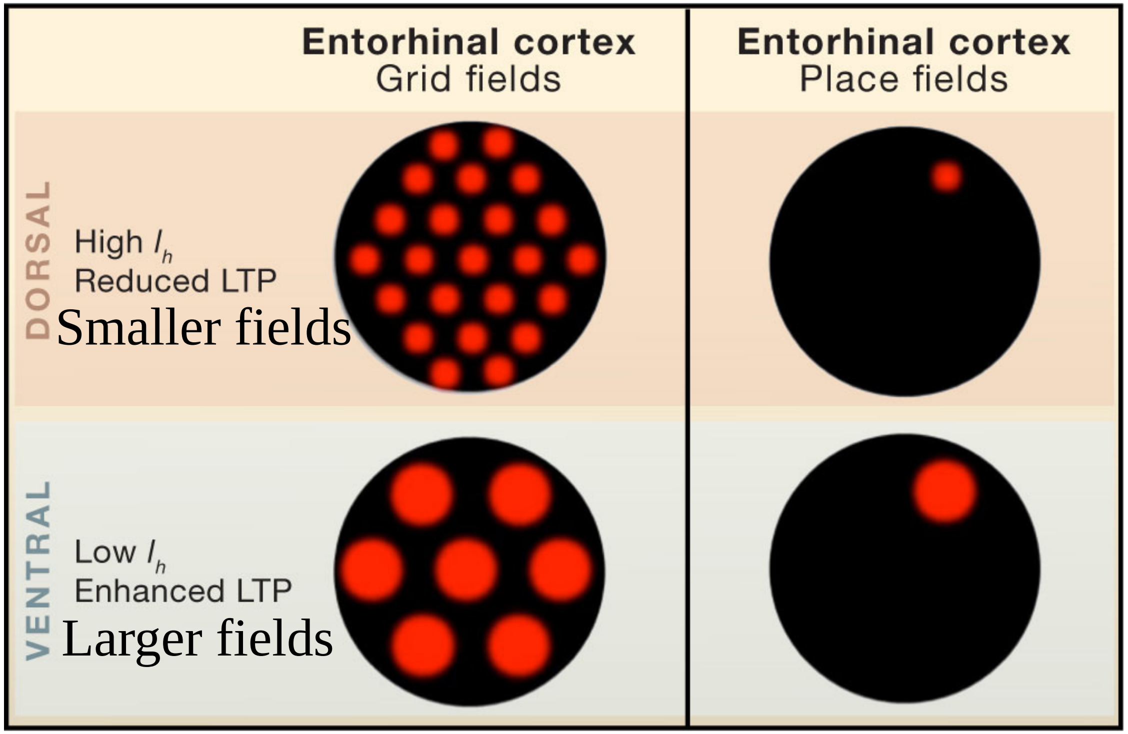




Z. Chen et al, *PLoS One (2011)*

O. Ahmed & M. R. Mehta, J. Neurosci (2012)

Asymmetric LTP model predictions for grid cells

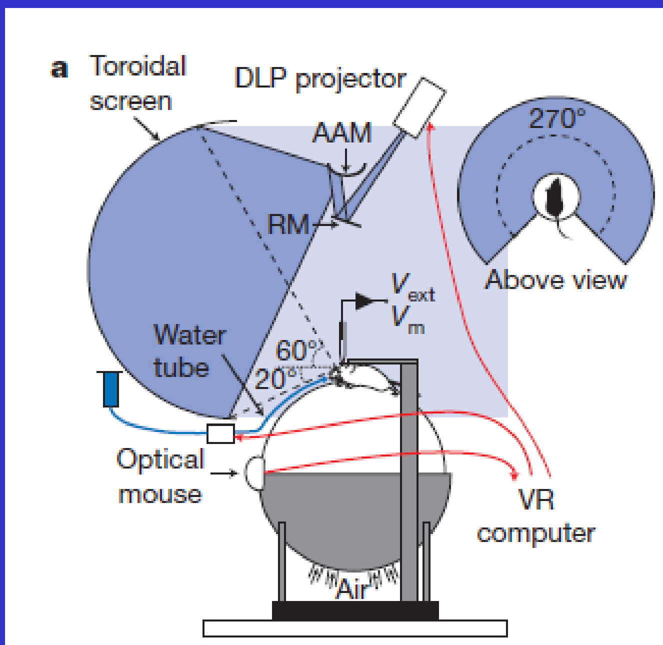


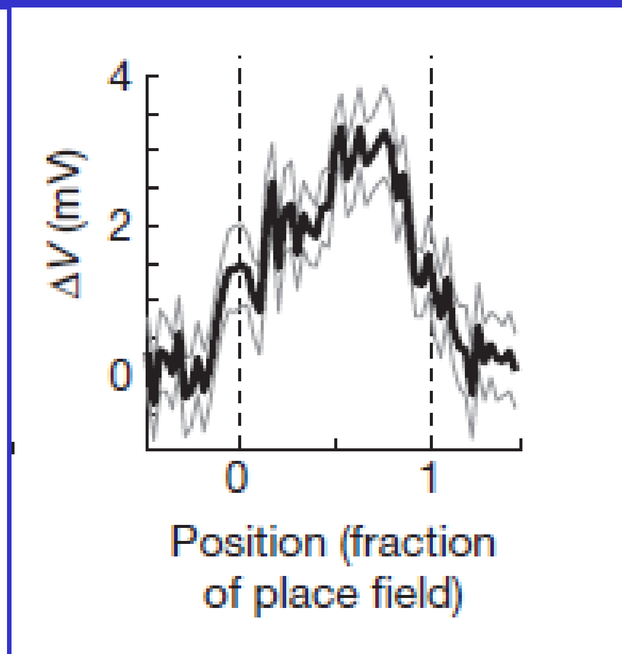
Mehta, Cell 2011

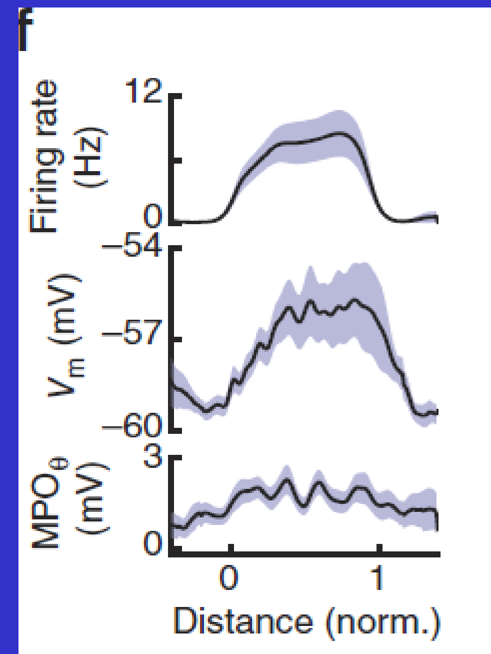
Based on Nolan/Kandel (2004) Giocomo/Hasselmo (2009) Hussaini/Kandel (2011) Giocomo/Moser (2011)

- Dorso-ventral gradient of grid fields could arise due to increasing temporal integration of synaptic inputs within grid cells with reducing *h* current along more ventral position in MEC.
- NMDAR-dependent synaptic plasticity is *enhanced* due to reduced *h* current resulting in an *increase* in the asymmetry of grid field, experience-dependence of grid field asymmetry, phase precession, and navigational learning.

Asymmetric subthreshold membrane potential of CA1 place cells and MEC grid cells in 1D VR







Harvey, Tank et al. *Nature* 2009

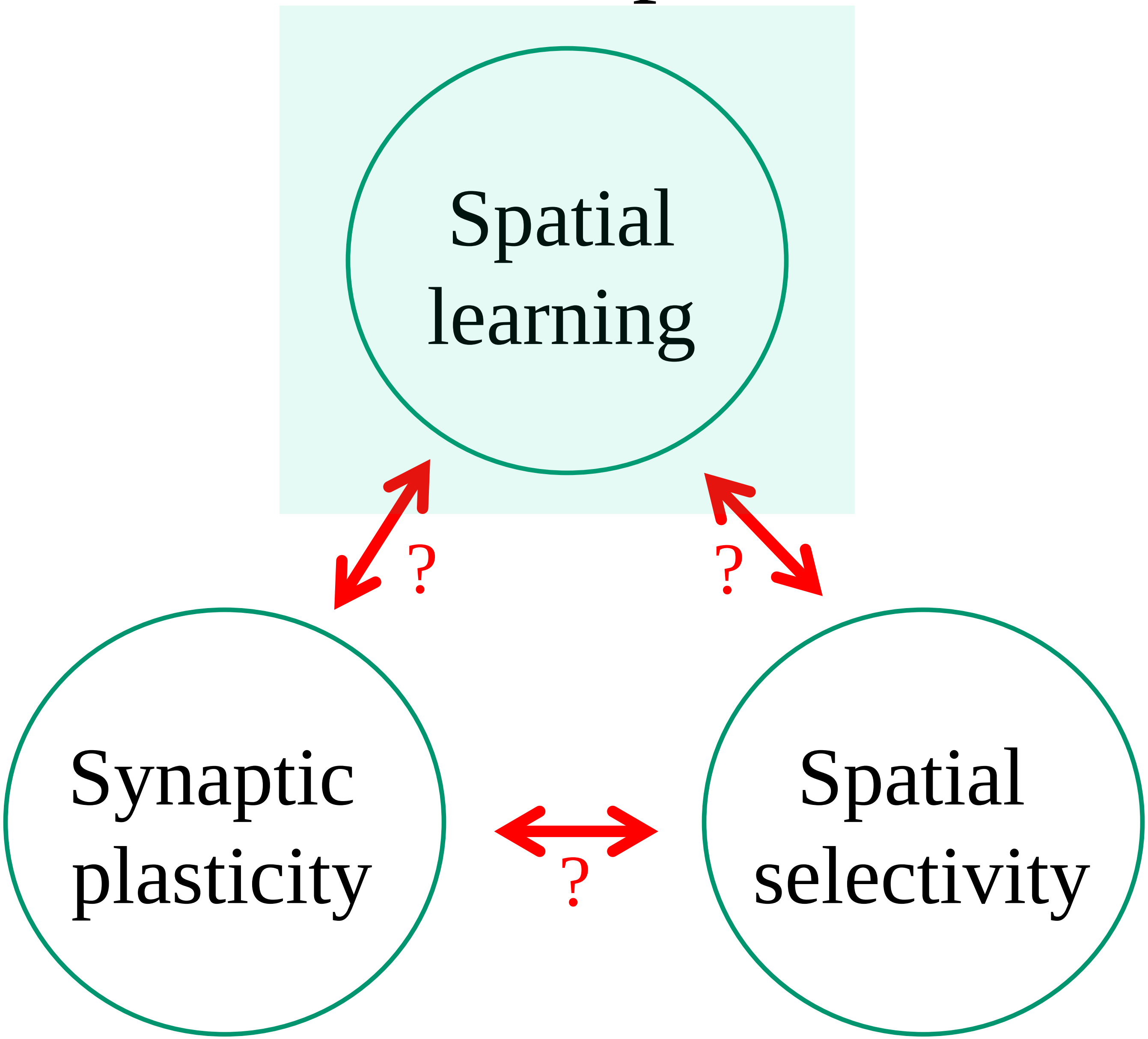
Schmidt-Heiber, Hausser

Nature neuro 2012

Intact spatial selectivity in 1D virtual reality in rats.

Also see: Domnisoru/Tank 2012, Chen/O’keefe 2013

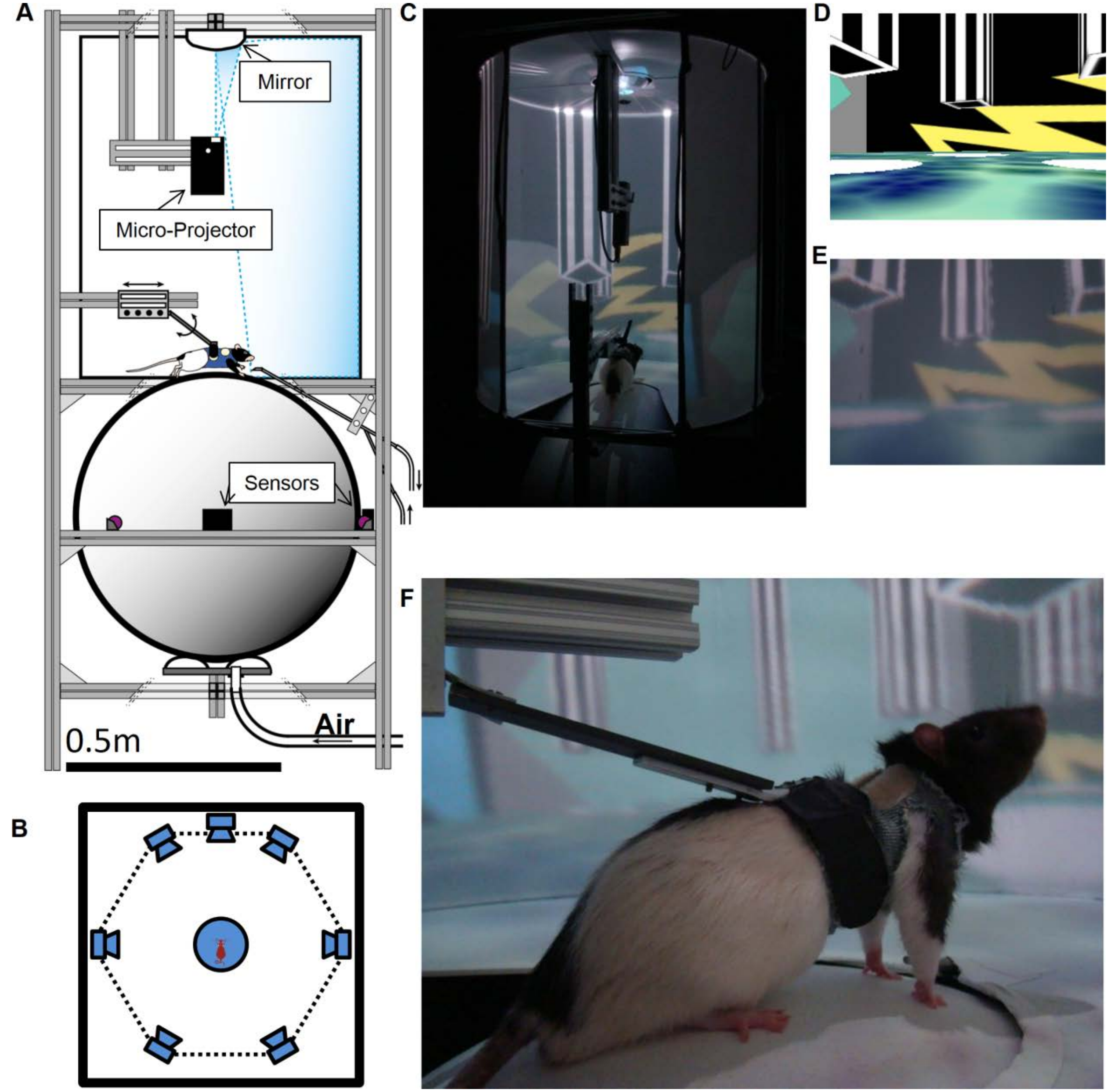
Mechanisms of spatial learning



Multisensory control of multimodal spatial behavior

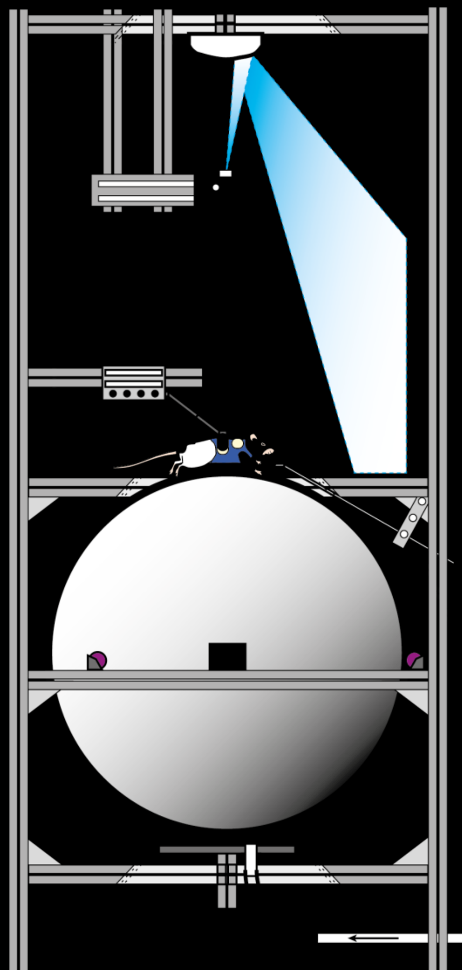
Multisensory maze: Audio-visual cues

Virtual soundscape in addition to virtual landscape



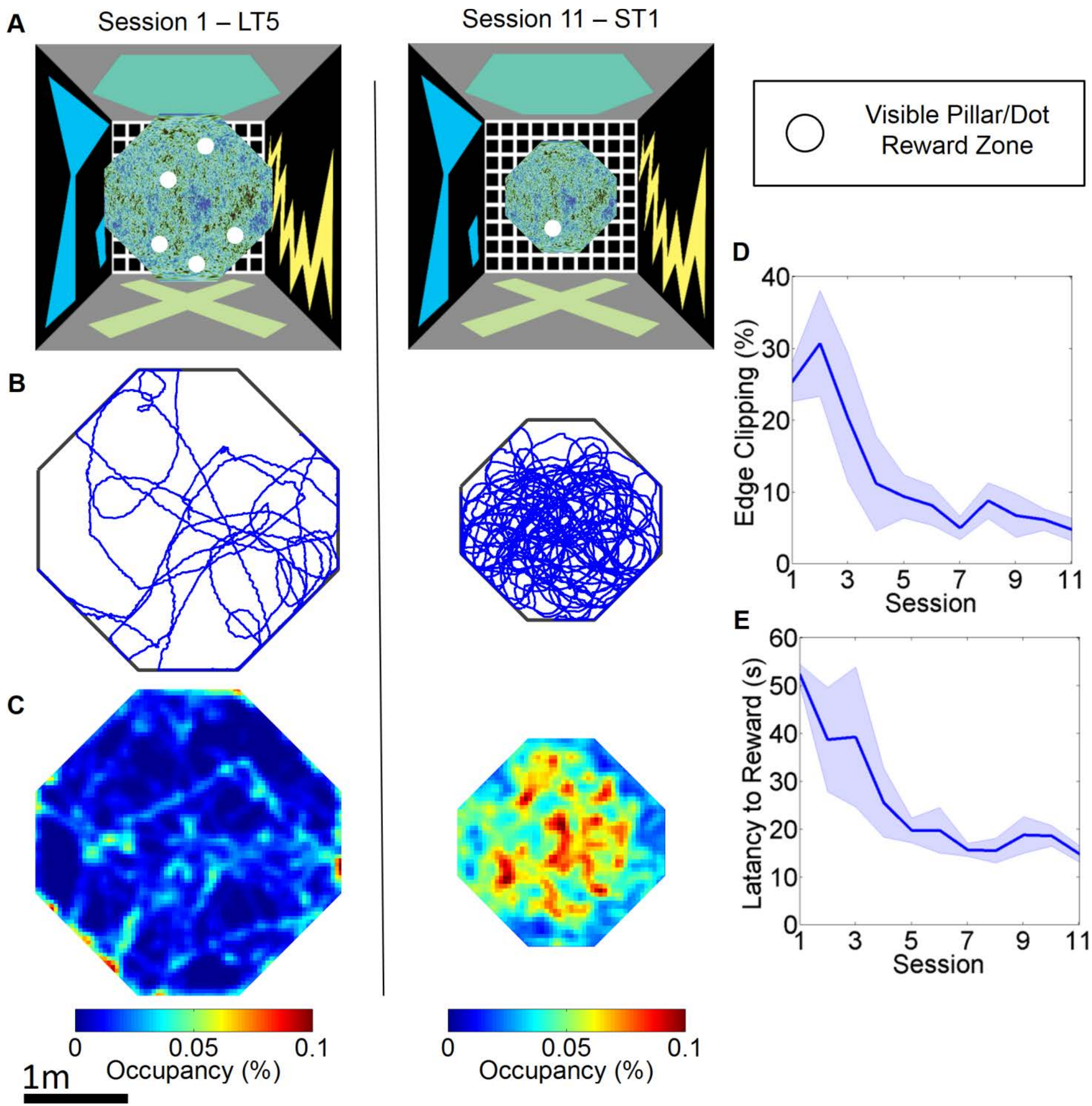
Cushman, Aharoni et al. PLoS1 2013

Noninvasive, Quiet, Virtual Reality System



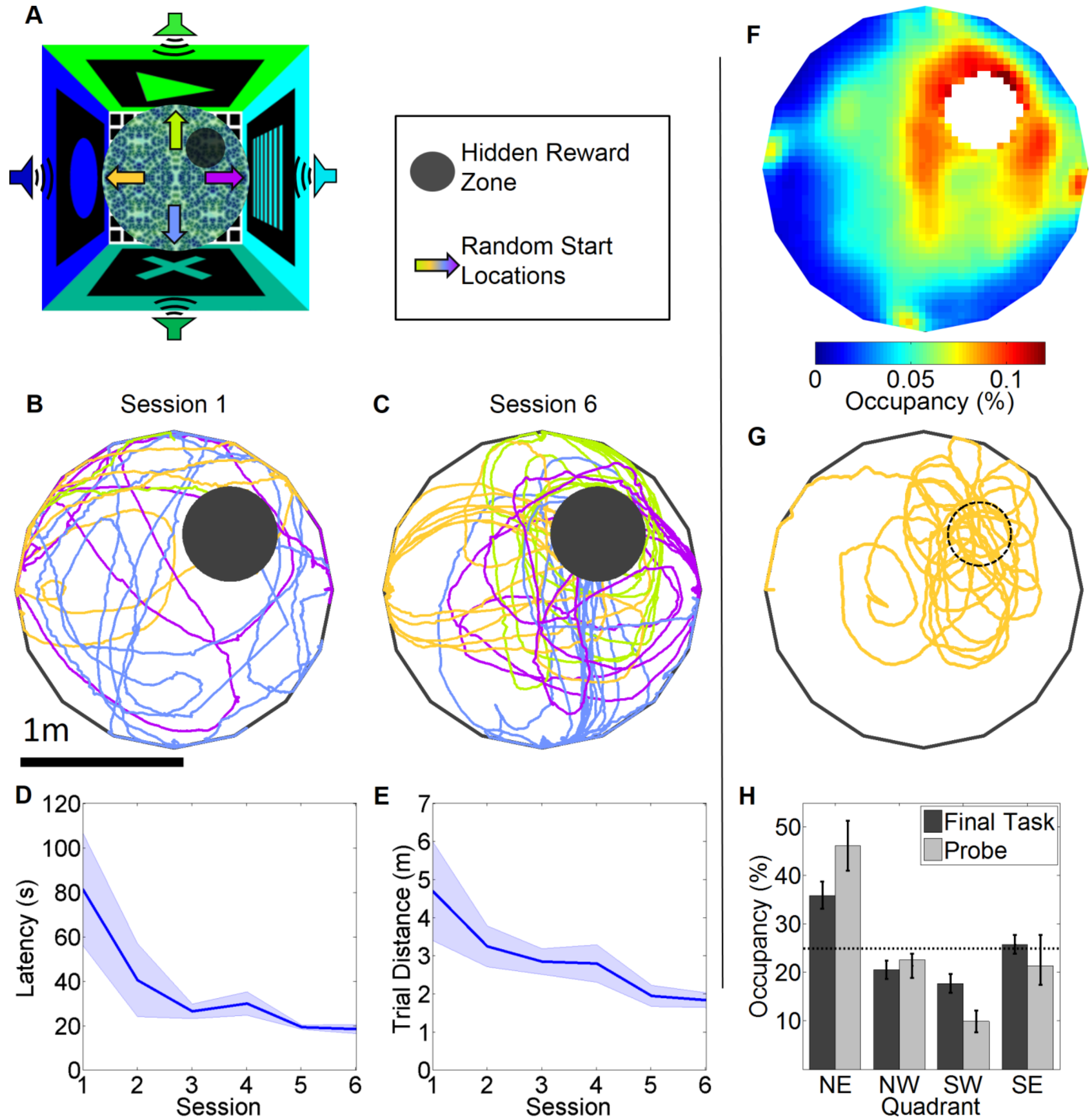
Aharoni, Willers, Arisaka, Mehta, Patent pending (2011)
Aharoni, Willers, Wang, Arisaka, Mehta, Patent pending (2011)

Rats can quickly learn virtual visual random foraging on a small platform and avoid edges



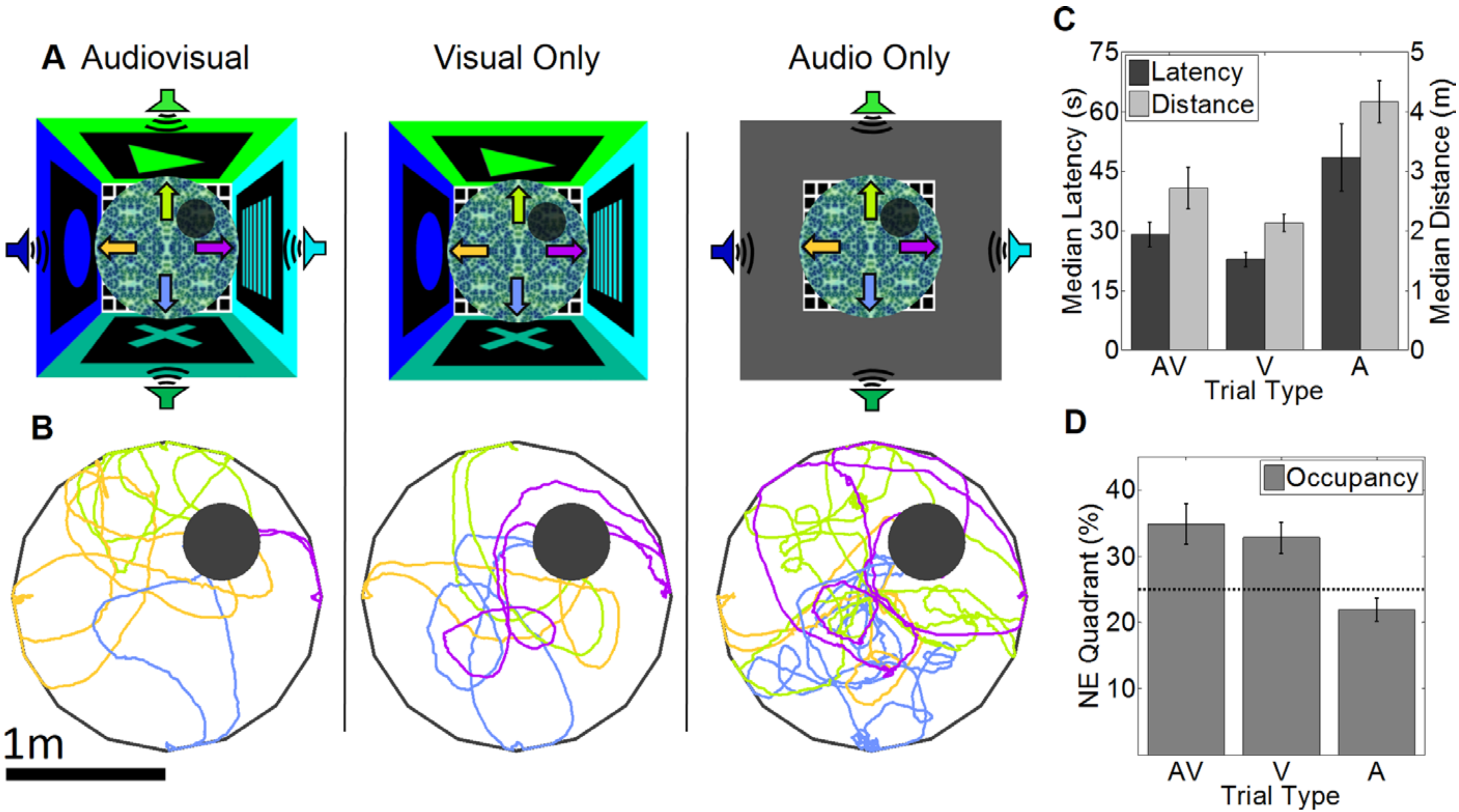
Cushman, Aharoni et al. PLoS1 2013

Rats quickly learn virtual audio-visual navigation, nearly as fast as in the real world water maze



Cushman, Aharoni et al. PLoS1 2013

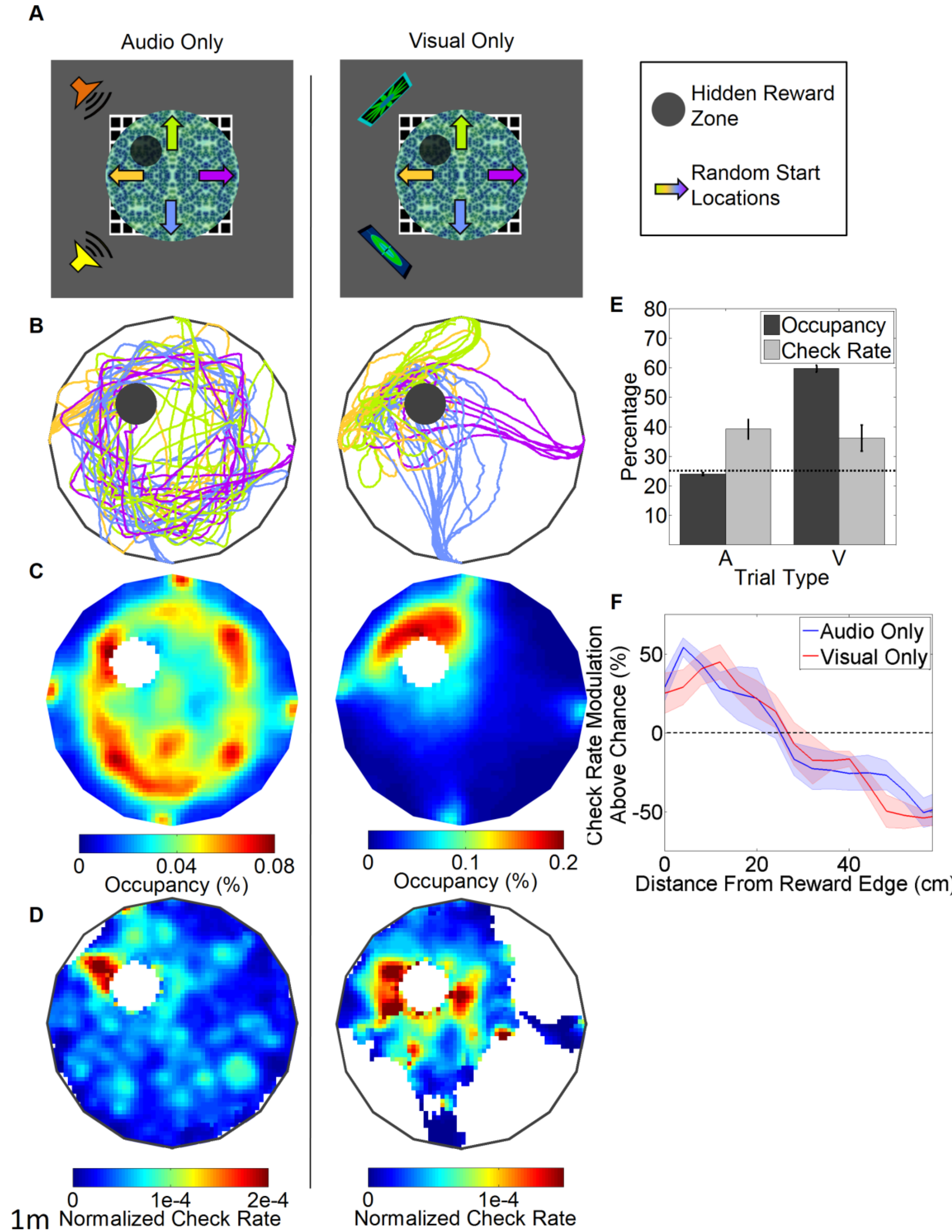
Visual stimuli are far more effective than auditory stimuli in generating spatial navigation map



Cushman, Aharoni et al. PLoS1 2013

With two visual cues rats learn navigational and reward expectancy maps

With two auditory cues rats learn equally precise reward expectancy map but don't learn navigational map



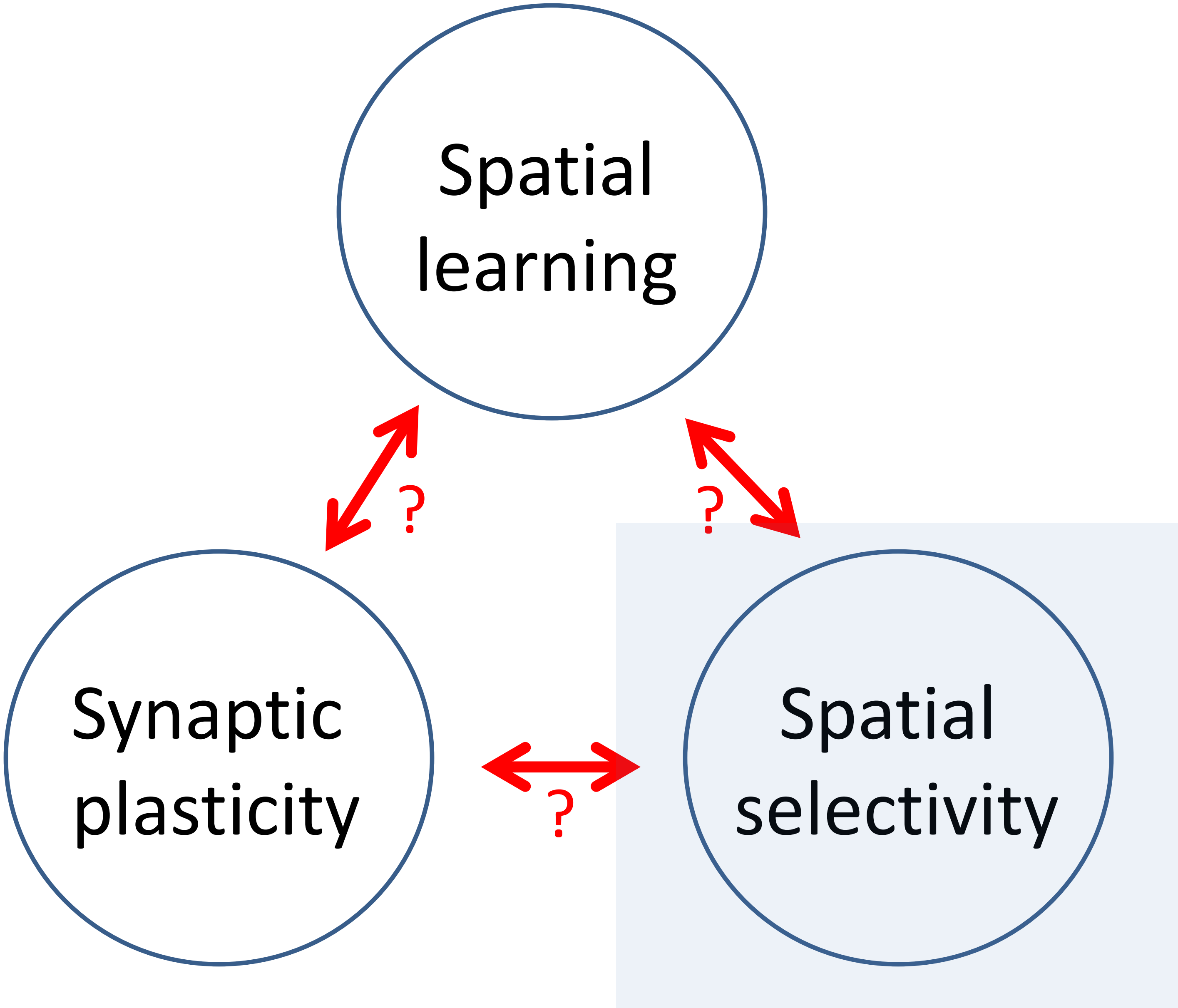
Cushman et al. PLoS1 2013

Conclusions and hypotheses

- Rats can readily learn to avoid virtual edges defined by purely visual stimuli without any somatosensation.
- Rats can learn a robust spatial navigational map based on only distal visual cues and minimal vestibular cues.
- Rats’ behavior simultaneously expresses reward expectancy map and navigation map.
- Rats are unable to learn a robust navigational map with four or two auditory cues.
- But, reward expectancy map with auditory cues is as accurate as with visual cues.
- The legs don’t always know what the tongue is doing.

Cushman, Aharoni et al. PLoS1 2013

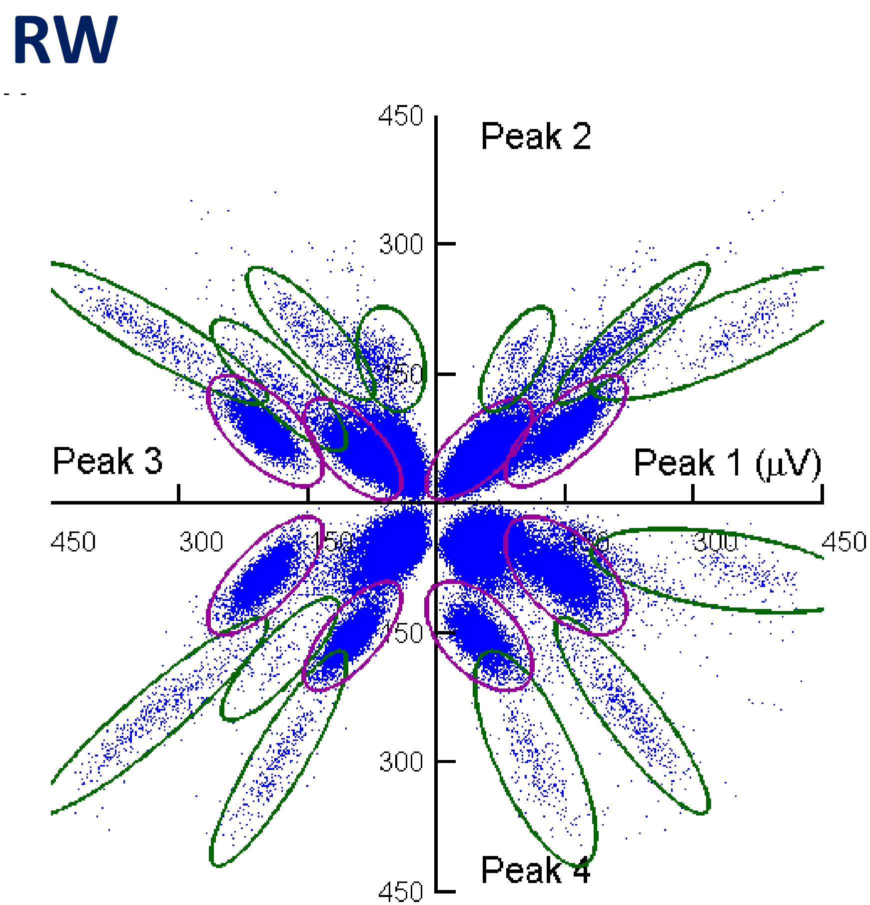
Mechanisms of spatial learning

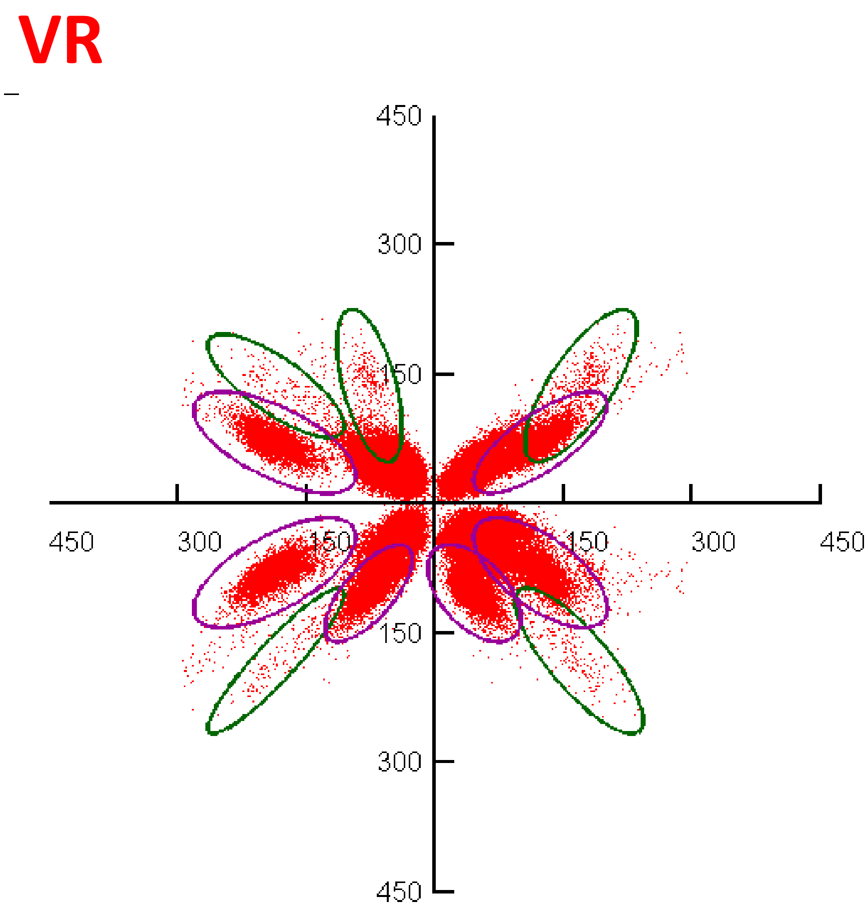


Contribution of distal visual cues and self motion cues to hippocampal spatio-temporal selectivity

Silence!

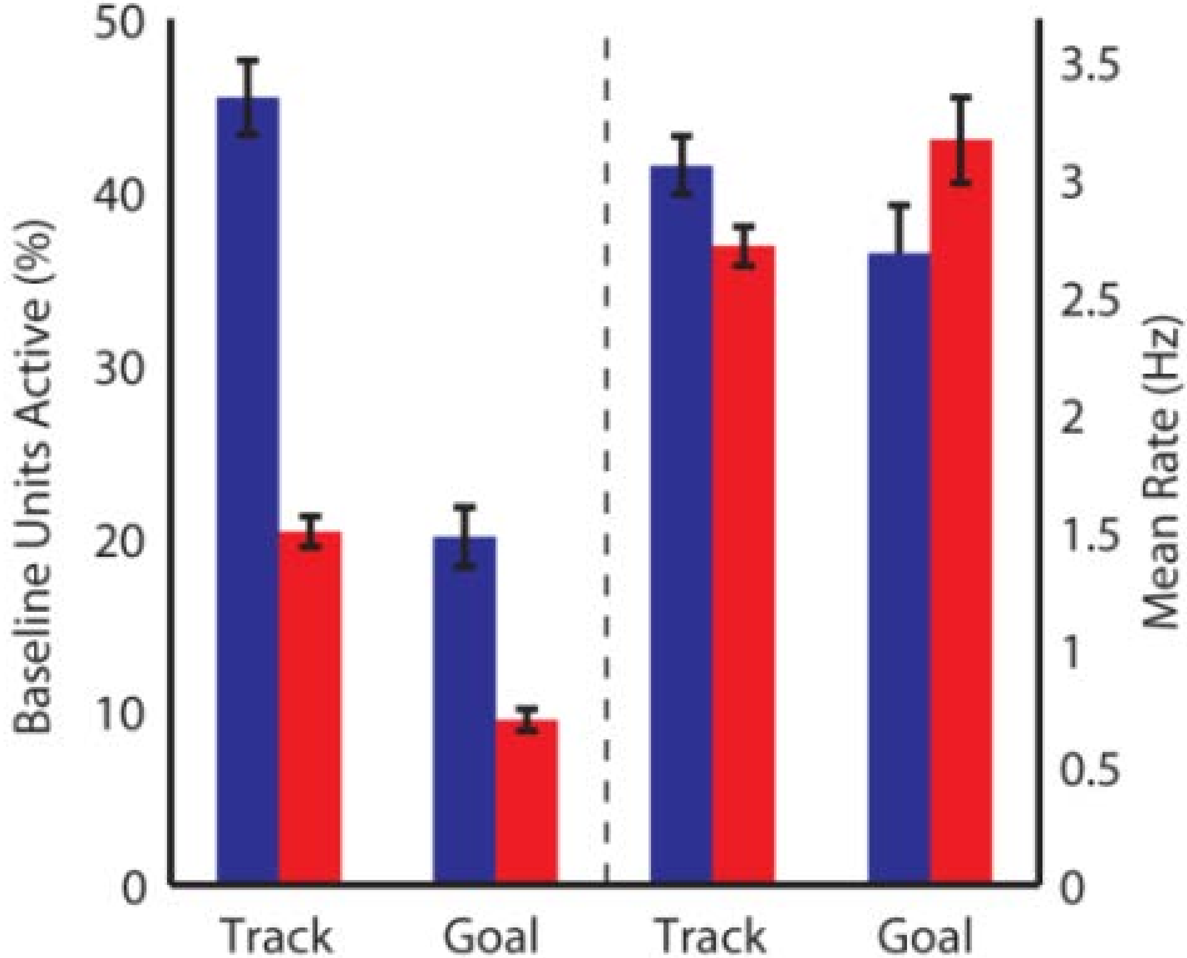
Following Results based on 2119 neurons from CA1



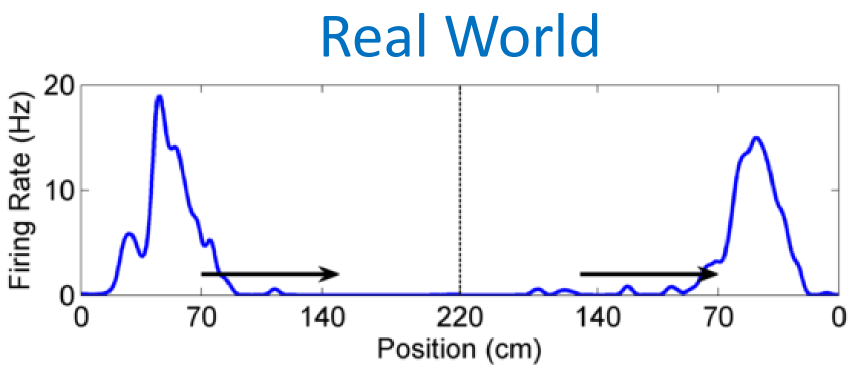


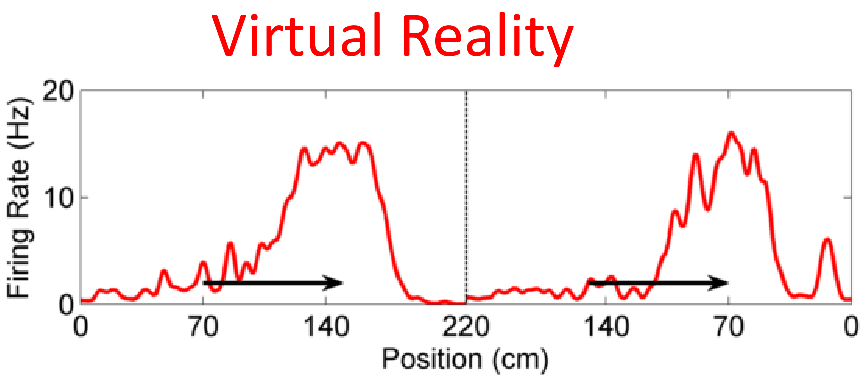
Ravassardd, Kees, Willers et al., Science, (2013)

Only half as many neurons are active in VR as in RW



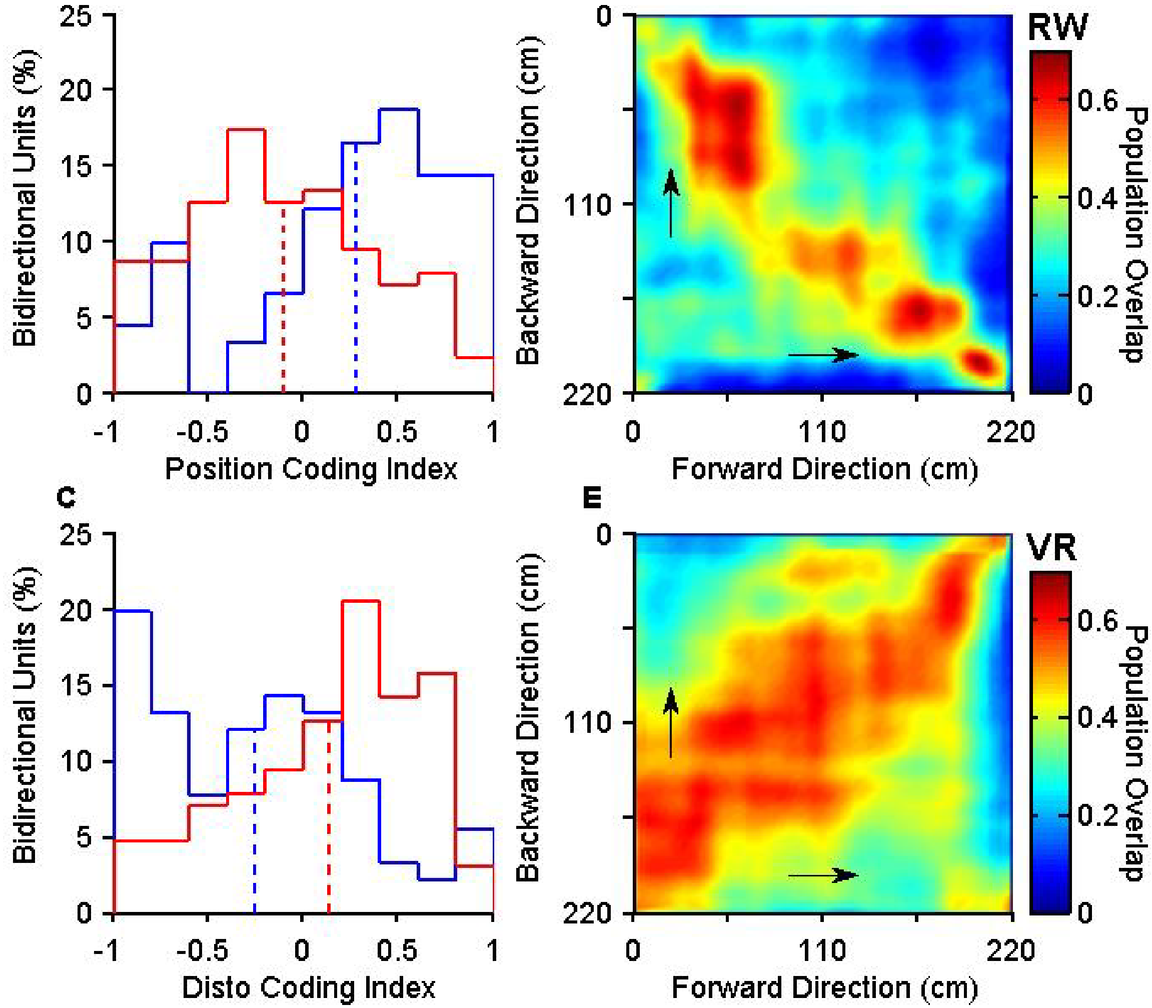
Competition: place cells in Real World show *place-code*, but in Virtual Reality show *Disto-code*





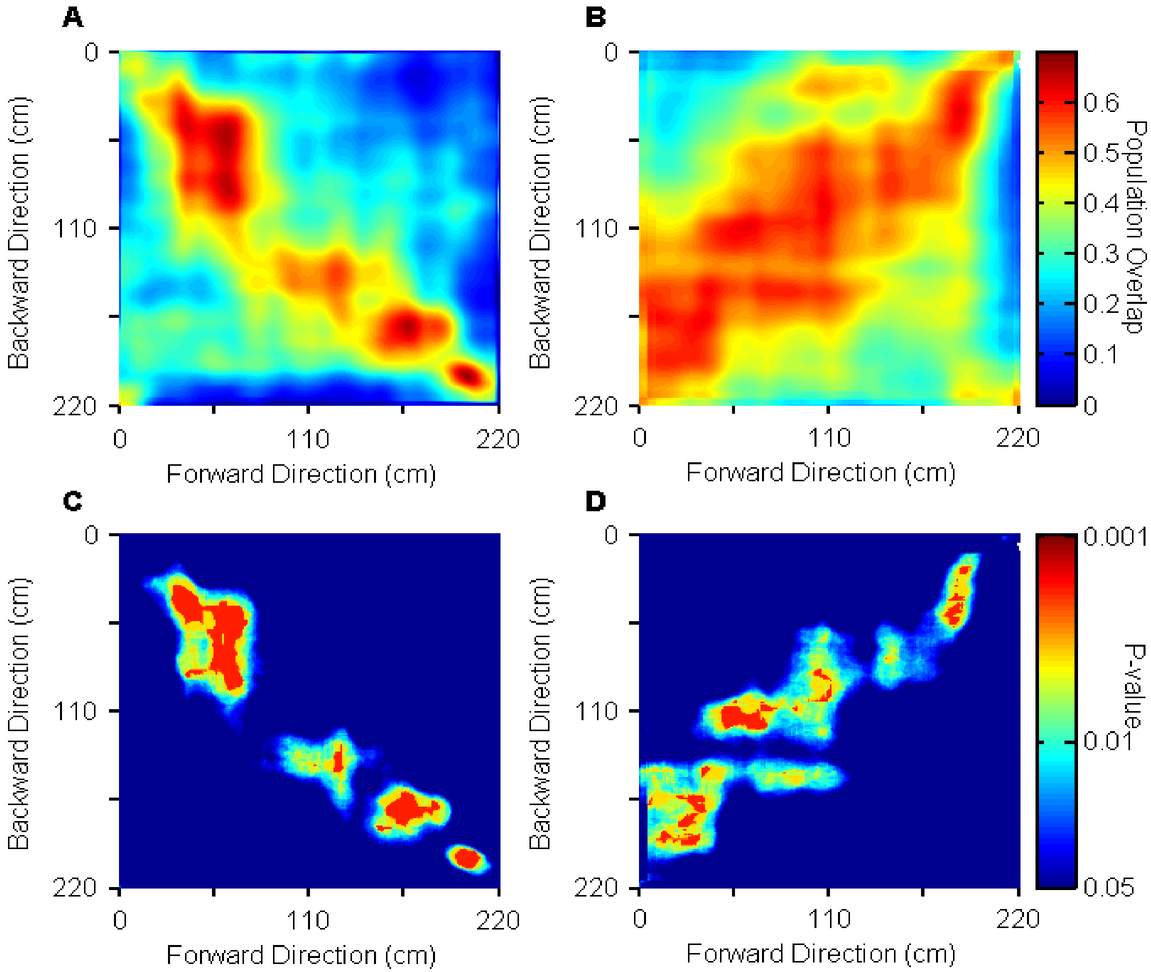
Ravassardd, Kees, Willers et al., Science, (2013)

Hippocampal ensemble code shows *position-code* in Real World but *Disto-code* in Virtual World

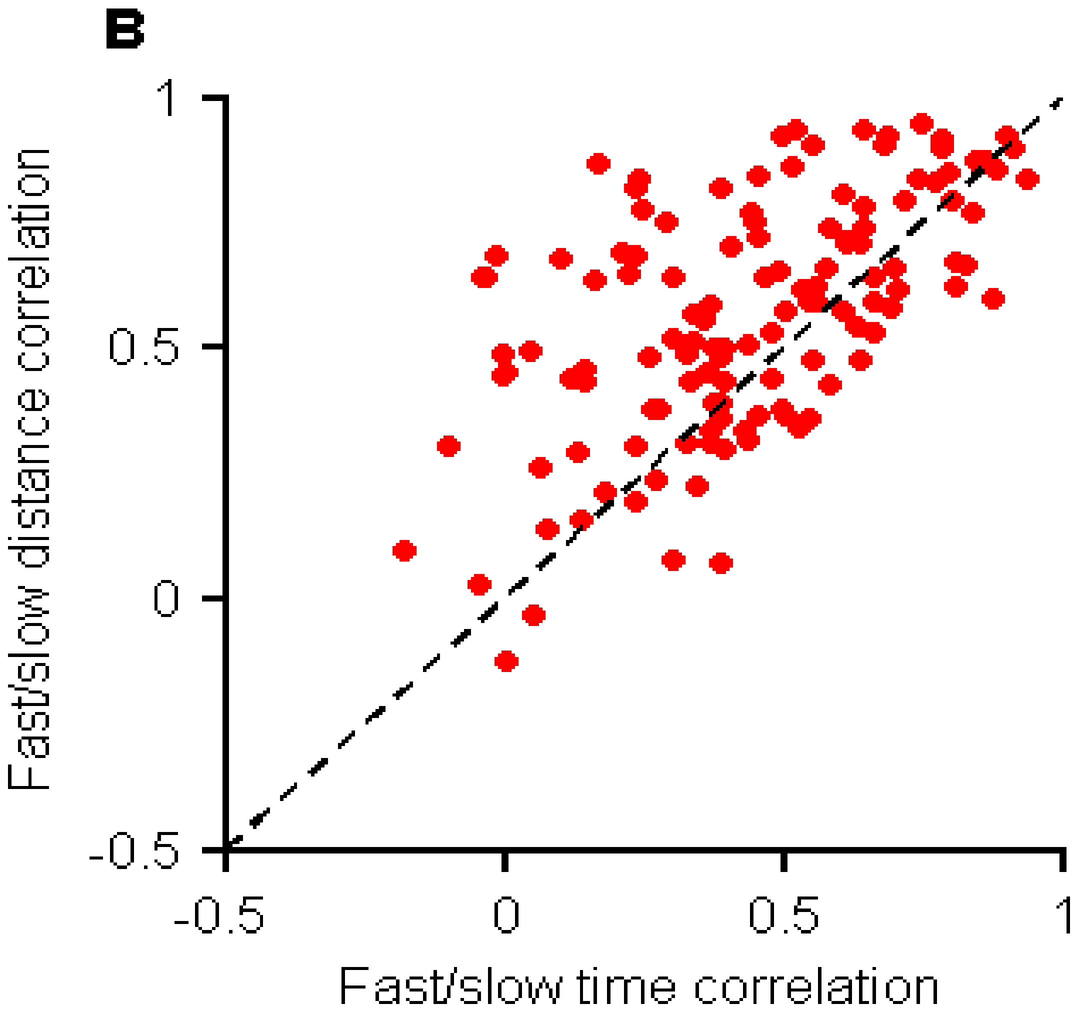


Ravassardd, Kees, Willers et al., Science, (2013)

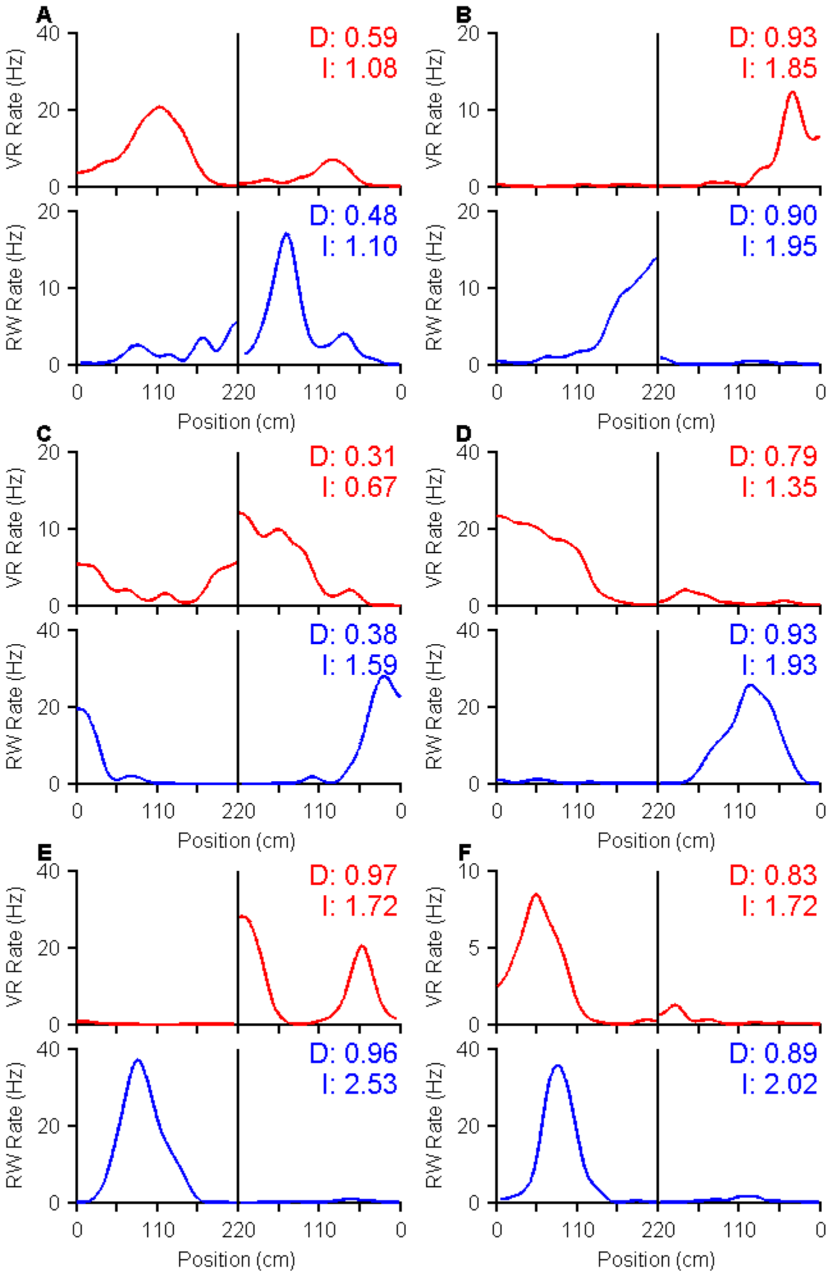
Control: Population vector overlap is significant only along the diagonal



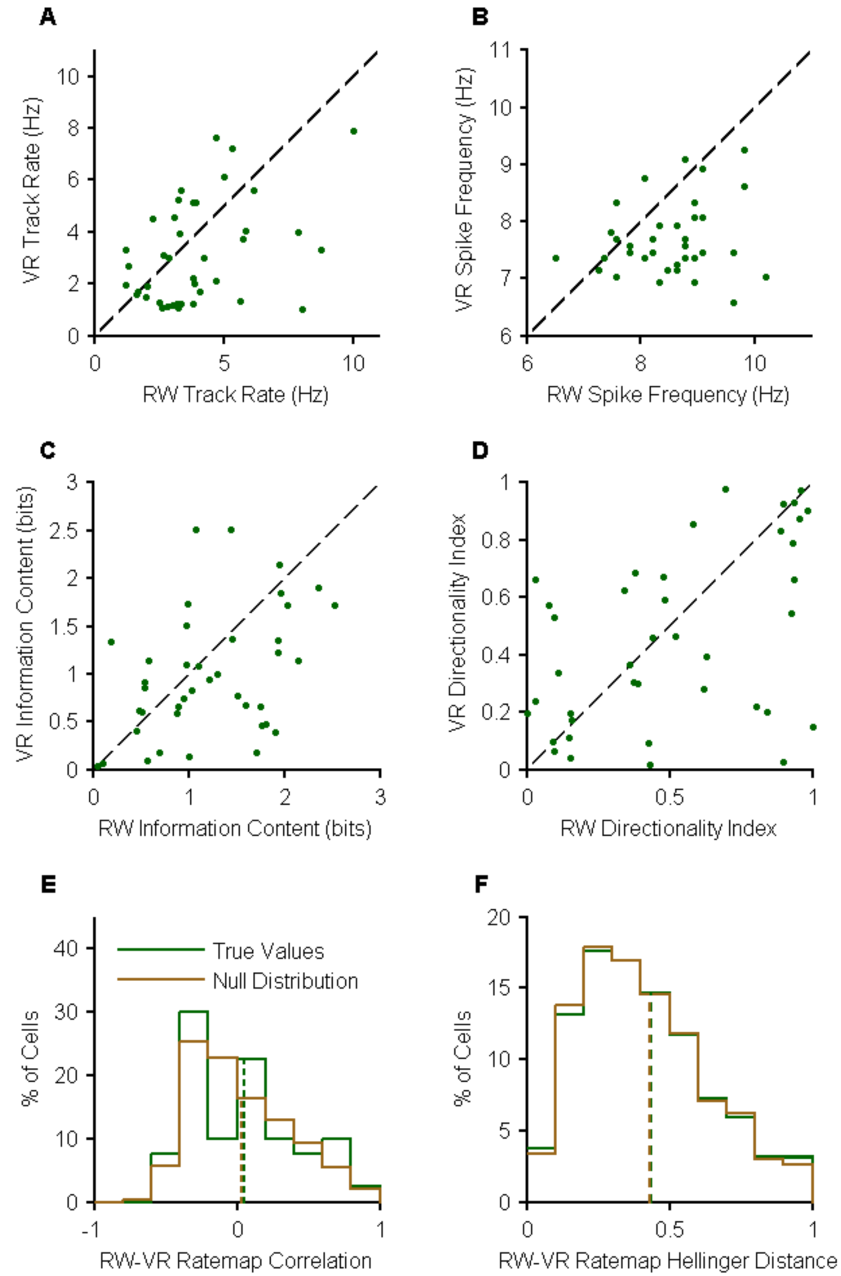
Control: Majority of cells seemed to code for distance not time elapsed



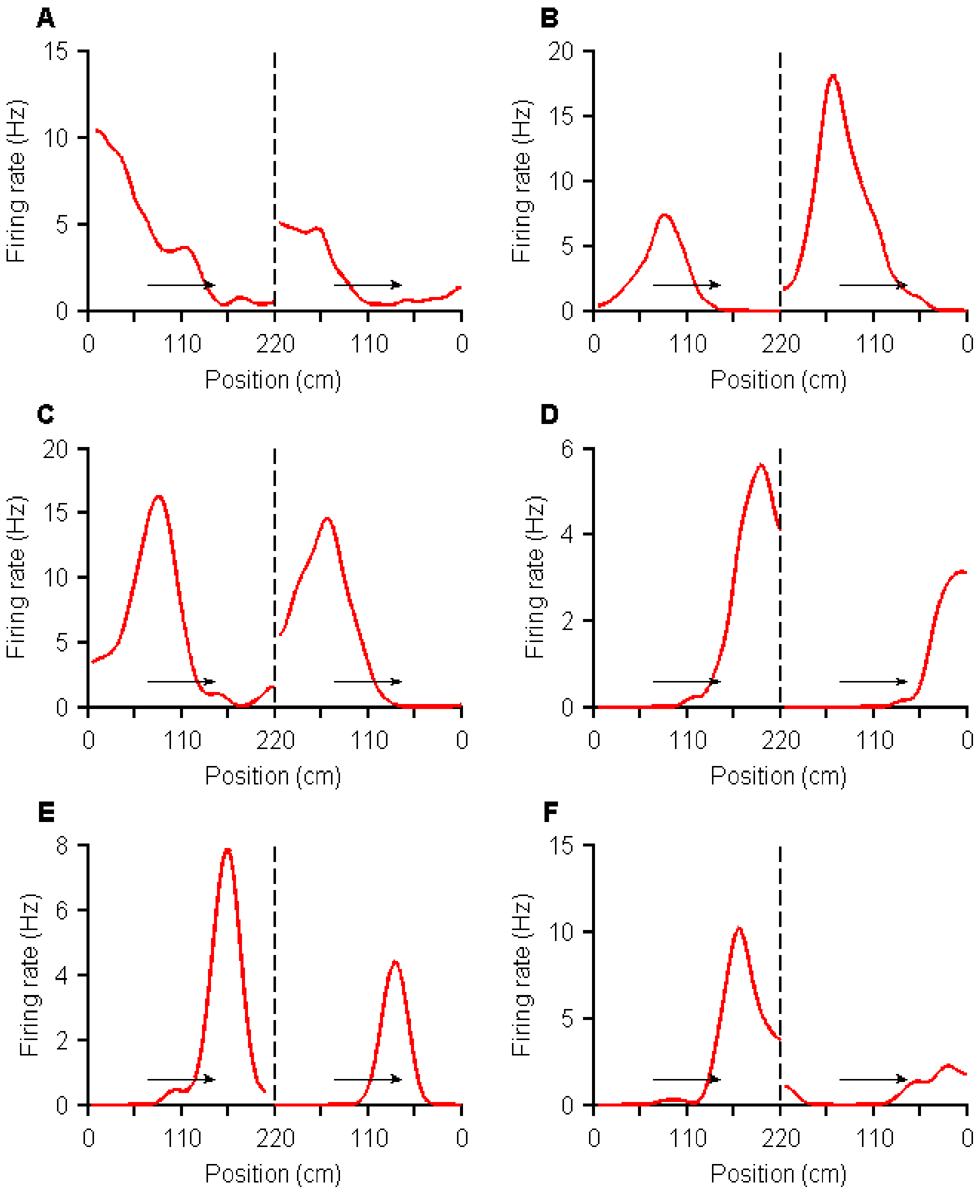
Control: Same cells show different spatial activity patterns in VR and RW



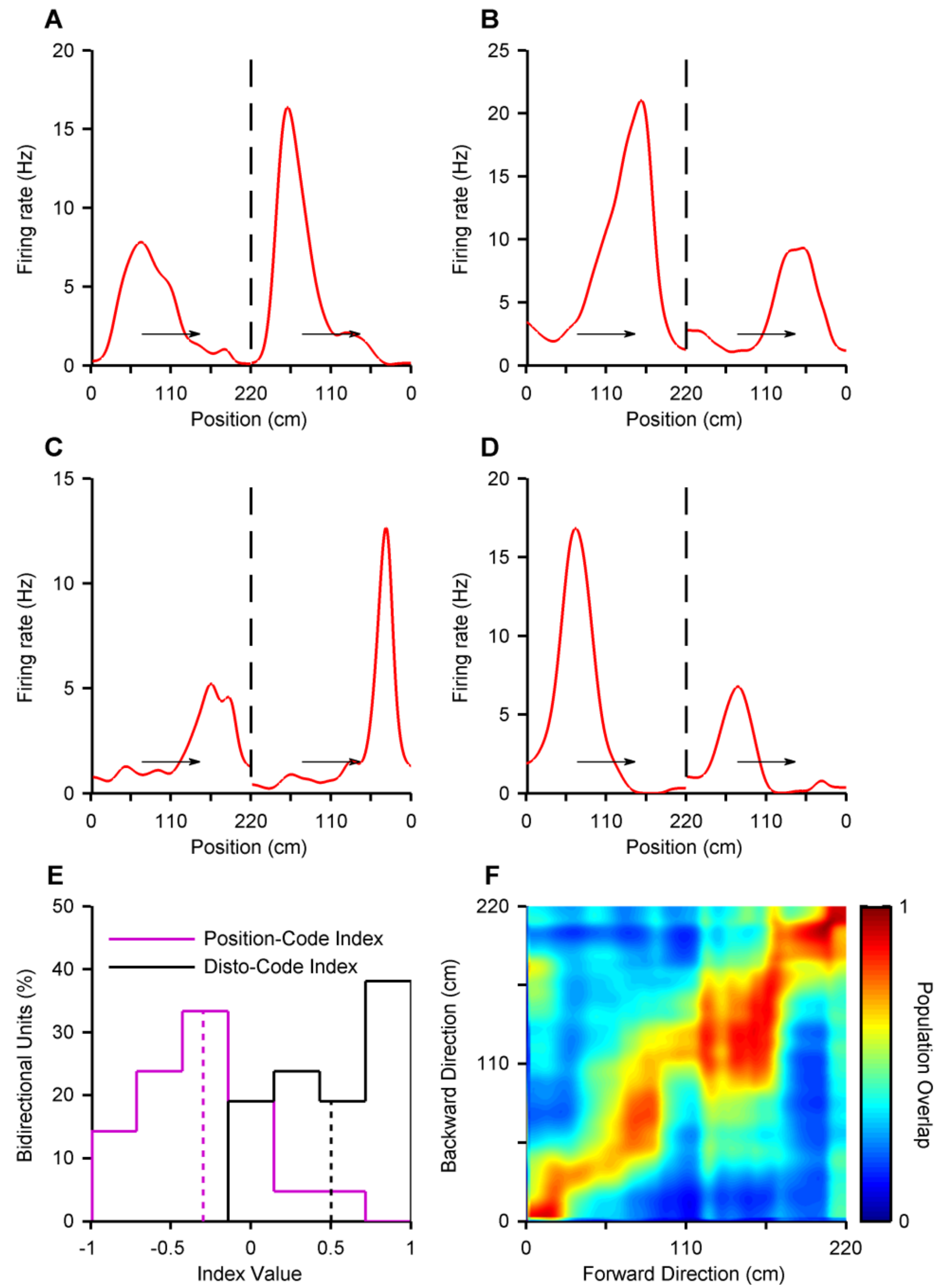
Control: Same cells have similar mean rate, spatial information and directionality, but spatial selectivity is uncorrelated between VR and RW



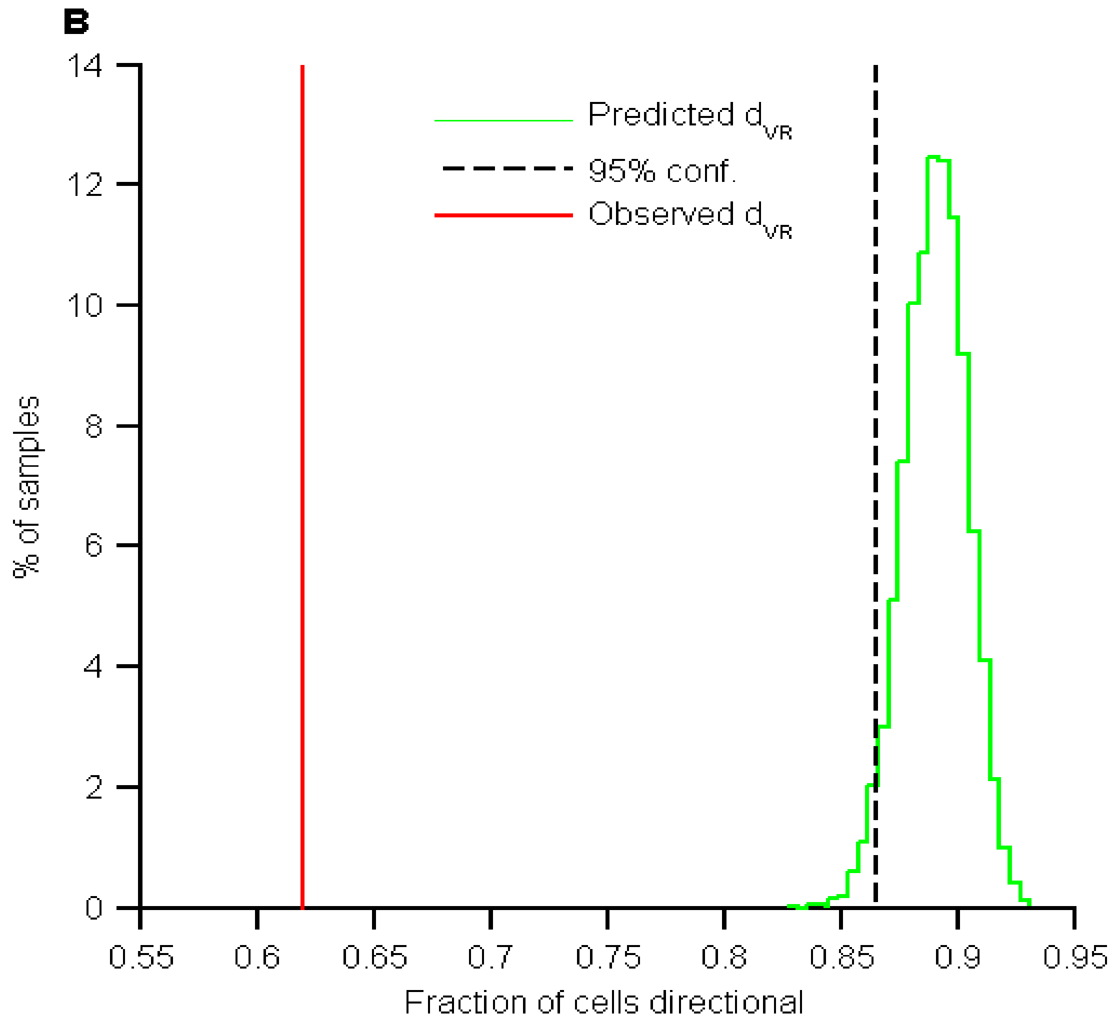
Control: Disto code is not due to the pillars at the track ends



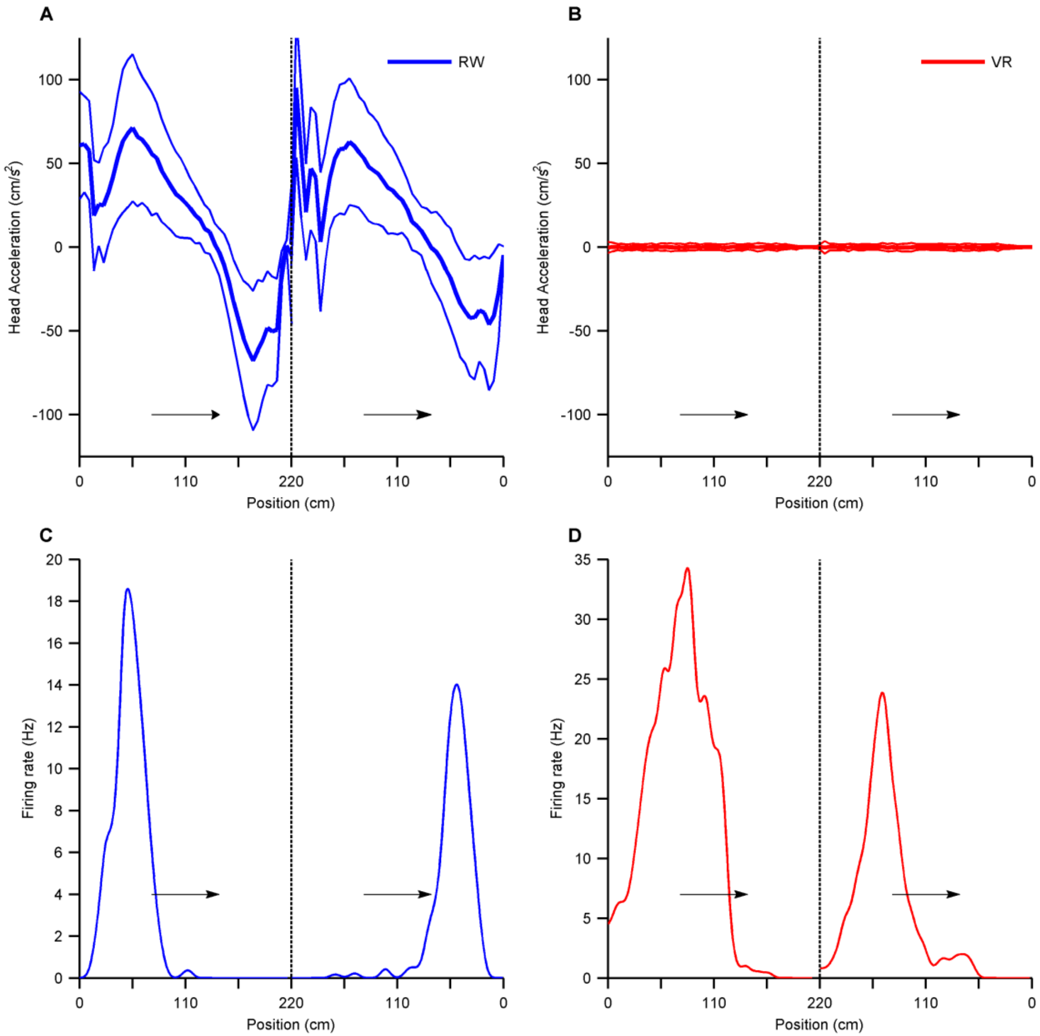
Control: Disto code is not due to passive scene reversal



Control: CA1 is not treating the two movement directions as independent worlds in VR



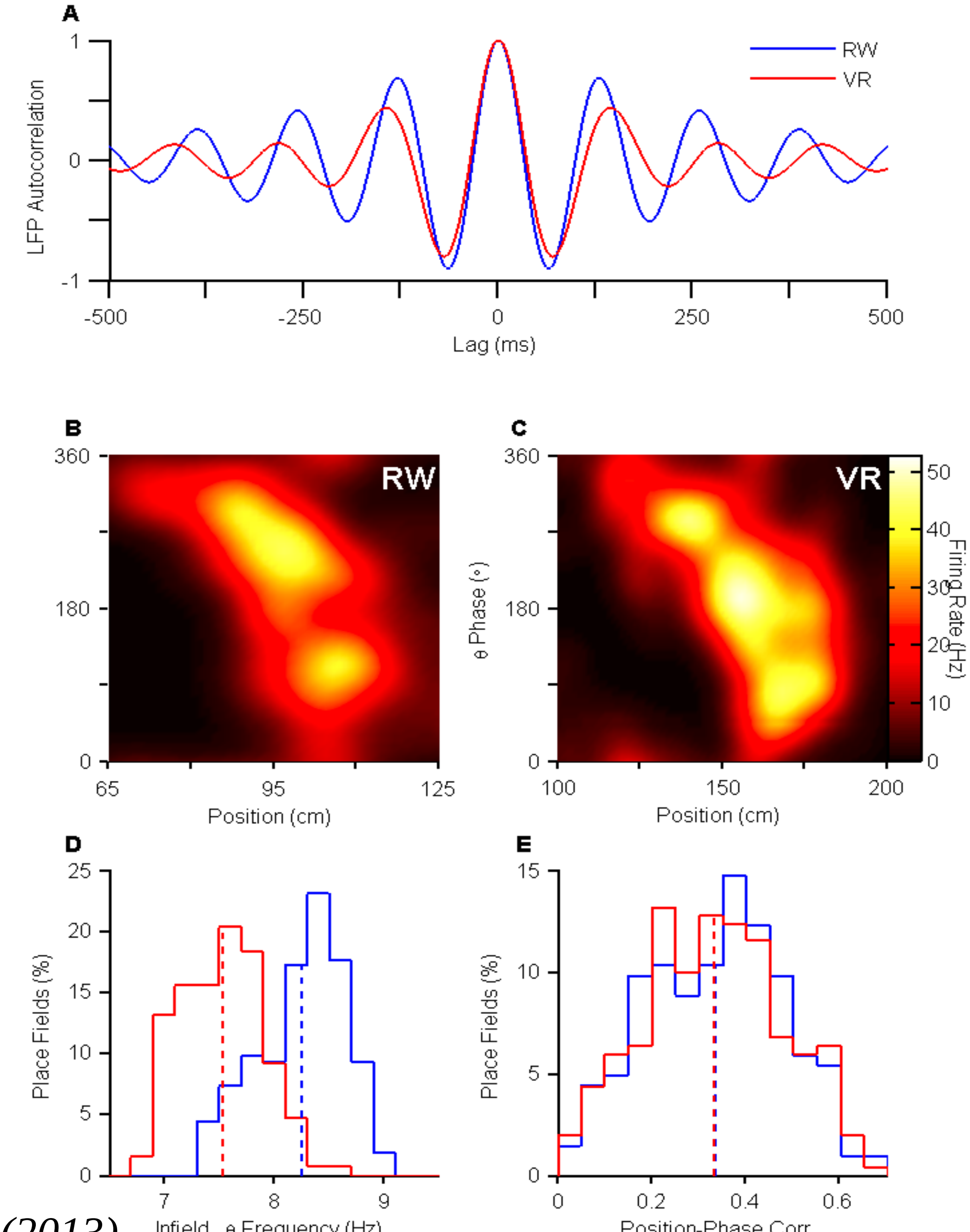
Control: Vestibular inputs should yield disto code in RW and its absence in VR



Conclusions and hypotheses

- Nearly 60% of neurons active in RW are silent in VR despite similar behavior and similar visual cues.
  - Distal visual stimuli are insufficient to drive CA1 robustly.
- Active neurons are *equally* directional in VR and RW.
  - Two directions of track treated similarly in VR and RW.
- Bidirectional neurons show an *absolute position* code in RW and *disto code* is suppressed.
- Bidirectional cells show a relative distance, i.e. *disto code* in VR and *position code* is suppressed.
- Other cues, e.g. olfactory stimuli on tracks, could generate more activity and absolute position code in RW.
- Locomotion cues+ distal cues generate disto code in VR.
- When spatially informative proximal cues are present (in RW) they have a veto power over locomotion + distal cues resulting in suppression of disto code in.

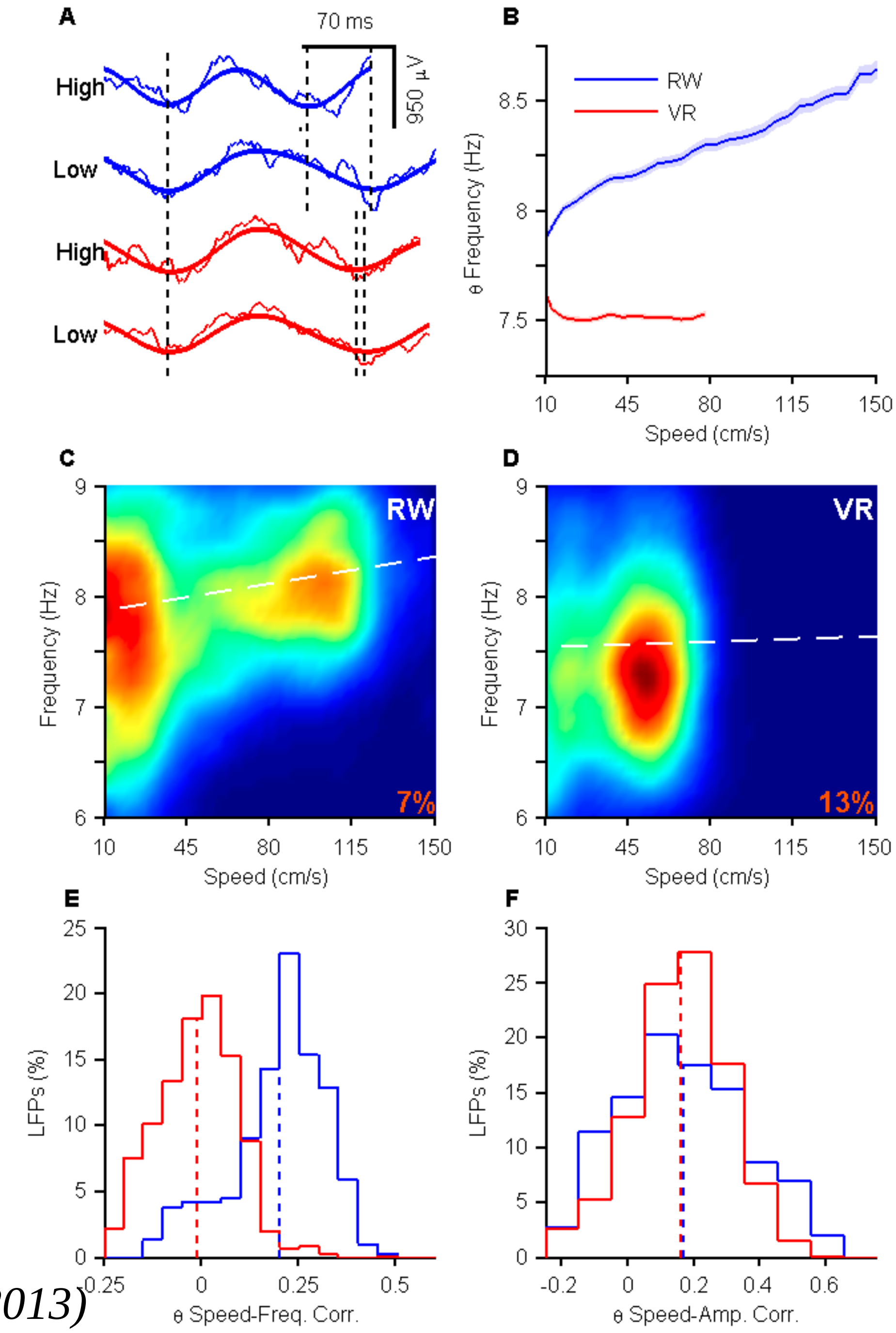
Reduced theta frequency in virtual reality but no change in hippocampal temporal code



Ravassardd, Kees, Willers et al., Science, (2013)

Theta frequency depends on speed in RW but not in VR.

Theta amplitude has similar dependence on speed in VR and RW



Ravassardd, Kees, Willers et al., Science, (2013)

Conclusions and hypotheses

- Speed-dependence of theta *amplitude* does not require non-visual and non-self motion cues.
- Speed-dependence of theta *frequency* is governed by cues that are non-visual and non-self motion.
- Phase precession does not depend on the speed-dependence of LFP theta *frequency*.
- Results consistent with asymmetric ramp + theta inhibition model of phase precession.

Ravassardd, Kees, Willers et al., Science, (2013)