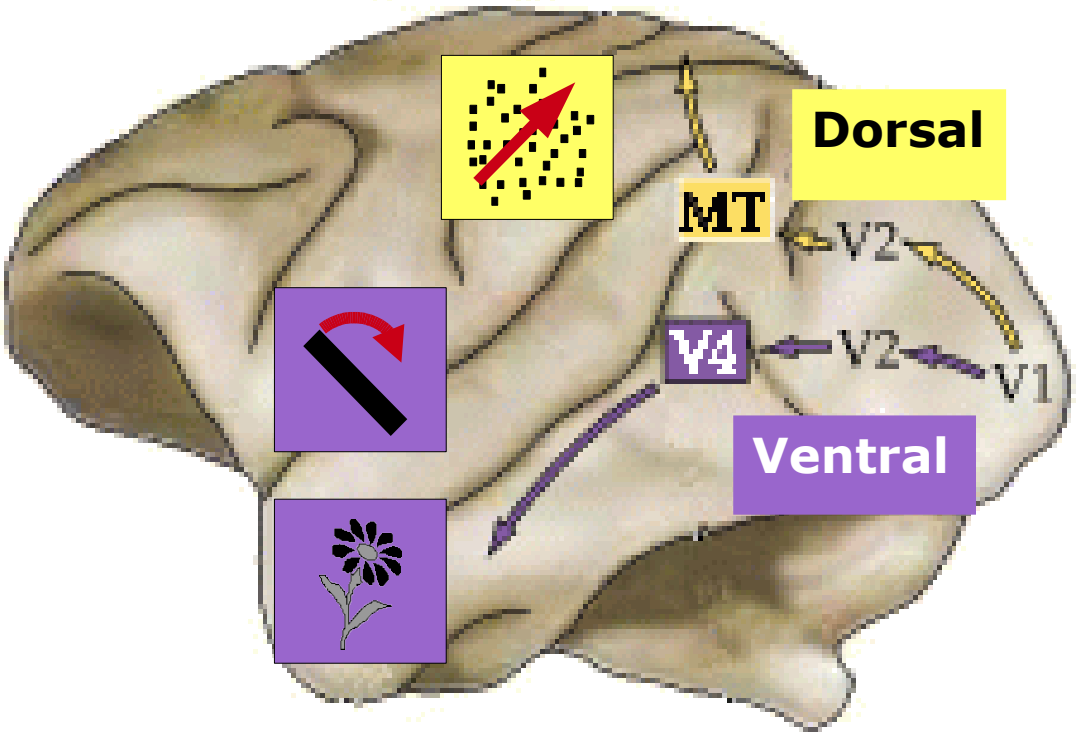
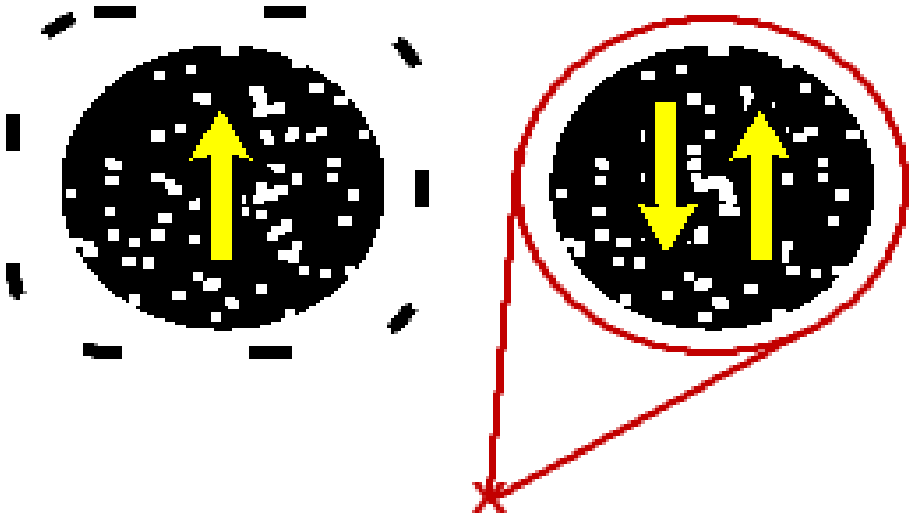
A sensory-executive circuit model of visual selective attention

Albert Compte

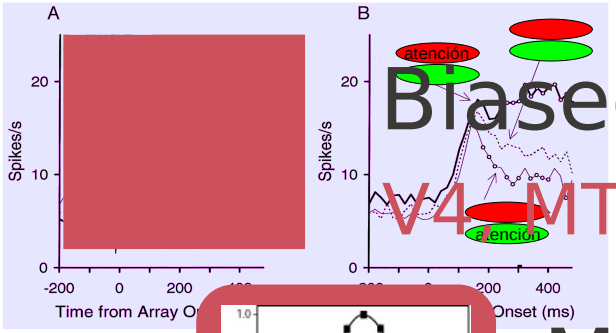
KITP, 1/10/2010

IDIBAPS


Dorsal
MT
V2
V4
V2
V1
Ventral

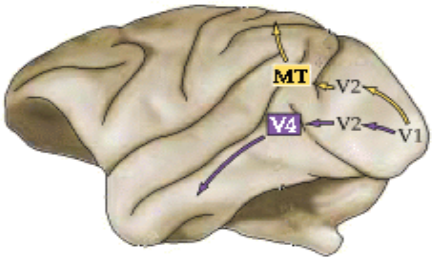


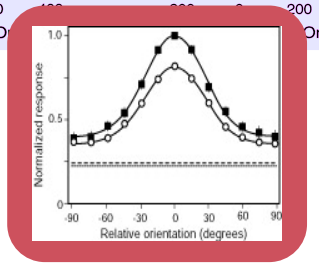
Neurophysiology of selective attention: observations



Biased Competition

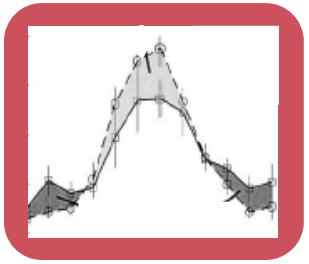
V4, MT





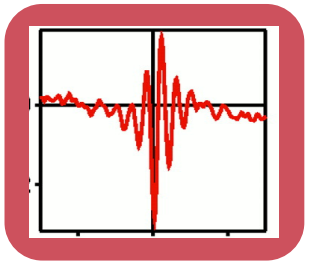
Multiplicative modulation

V4, MT



Selectivity enhancement

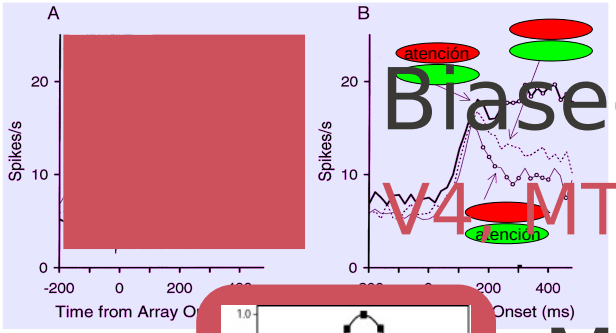
MT



Synchrony and oscillations

V4, MT

Neurophysiology of selective attention: observations



Biased Competition

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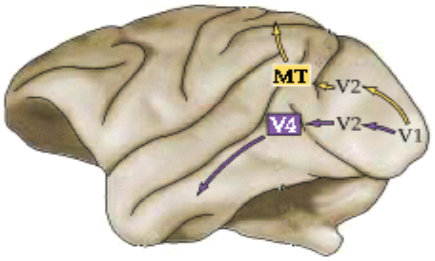
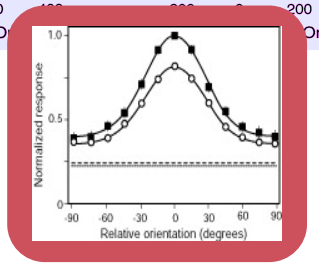
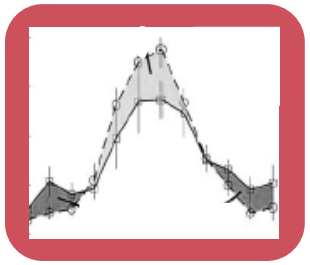




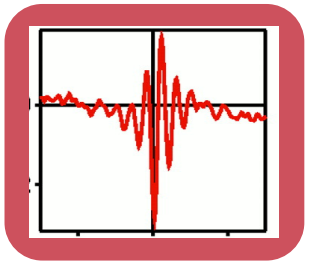
Multiplicative modulation

V4, MT



Selectivity enhancement

MT



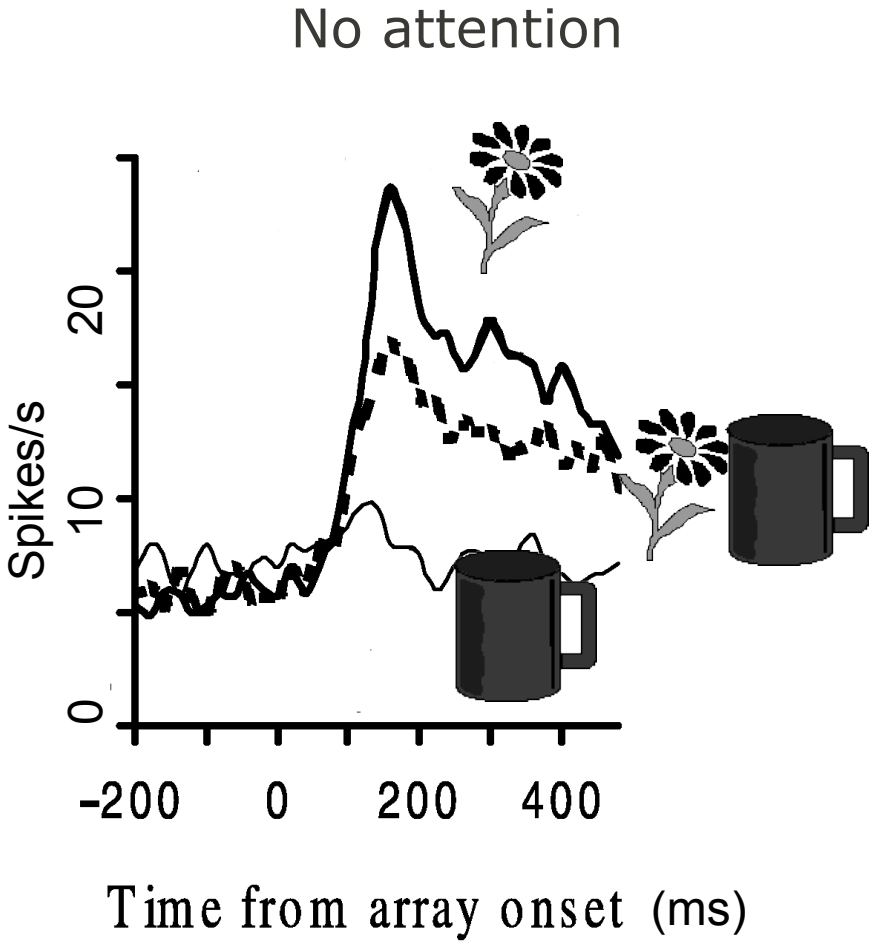
Synchrony and oscillations

V4, MT

Contrast and attention

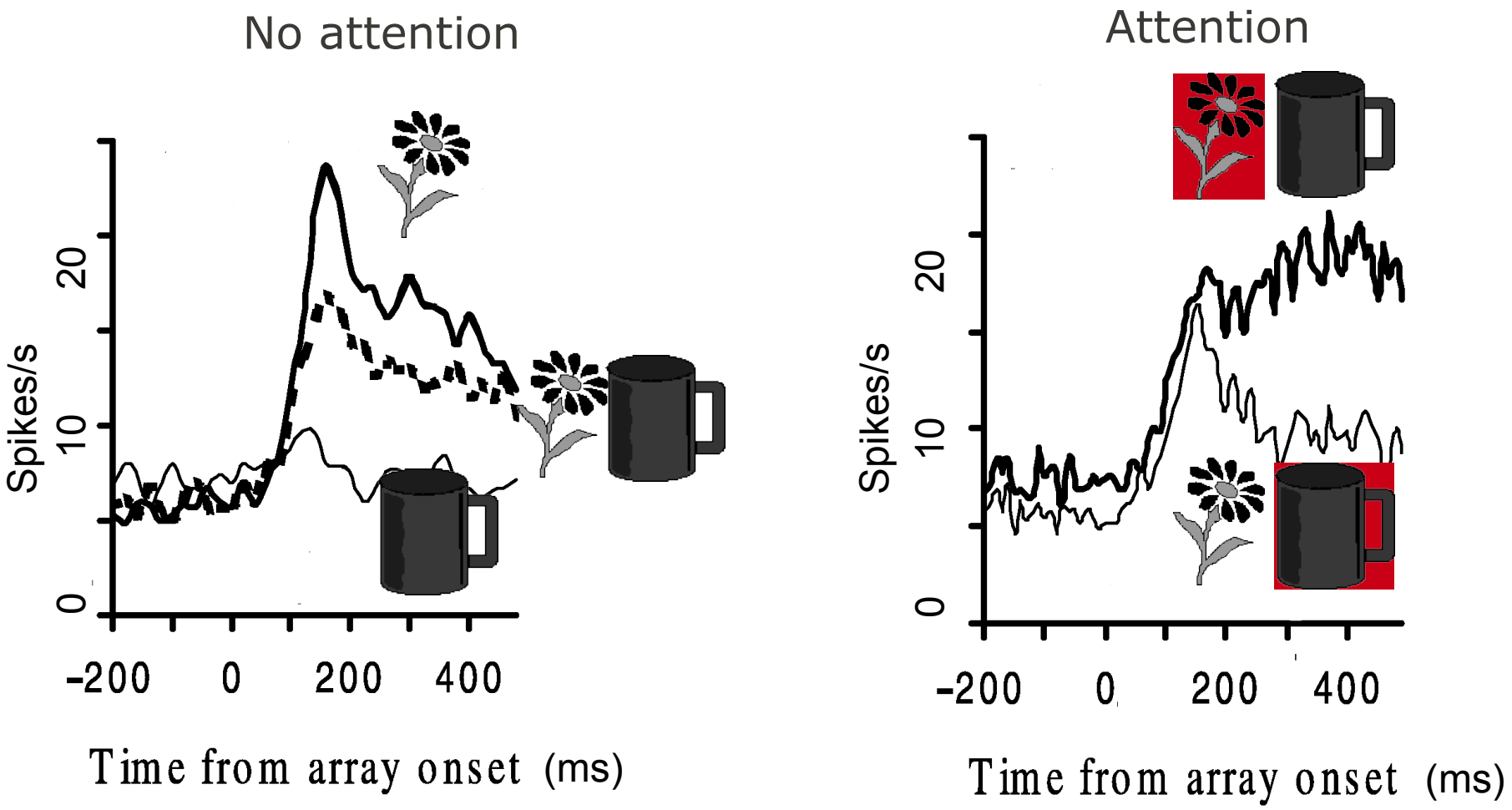
Correlations and attention

Biased Competition



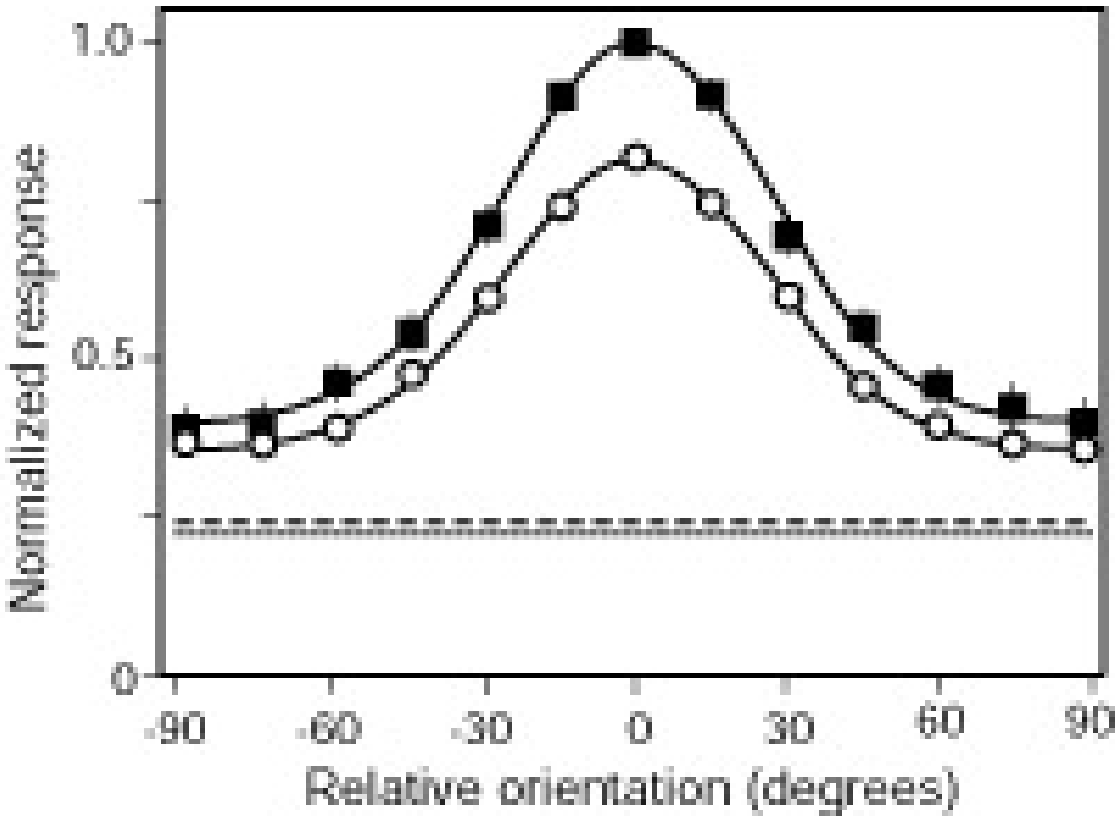
(Desimone and Duncan, *Annu Rev Neurosci* 1995)

Biased Competition



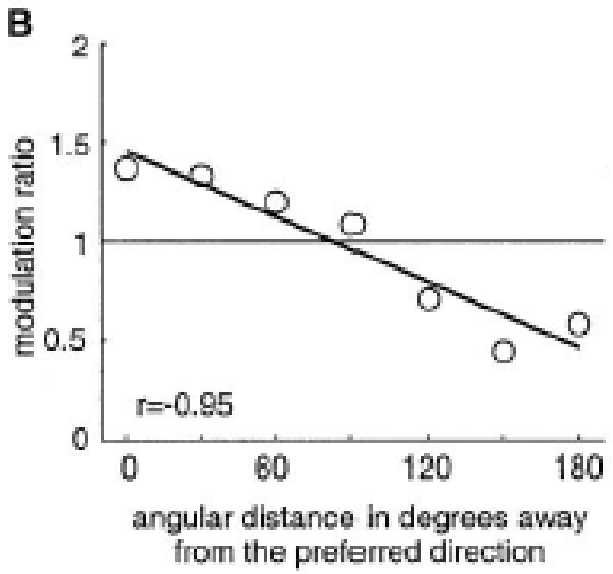
(Desimone and Duncan, *Annu Rev Neurosci* 1995)

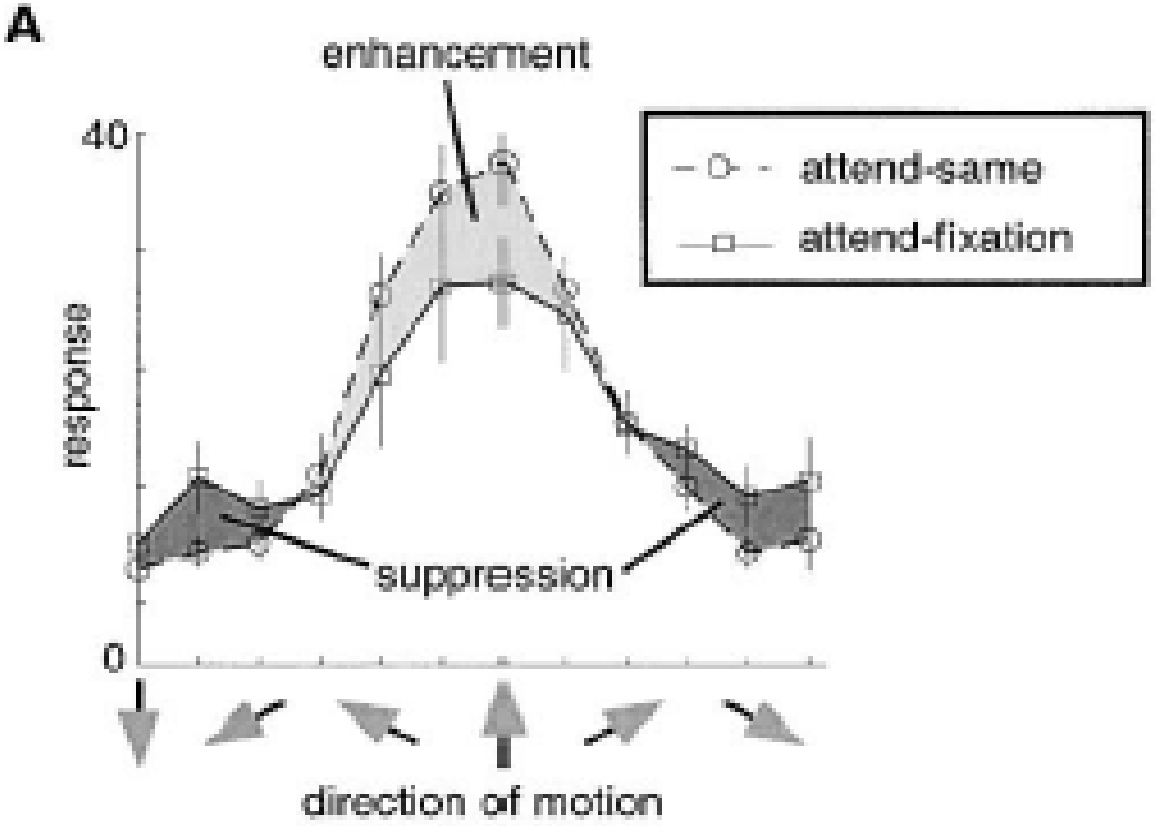
Multiplicative modulation



(McAdams and Maunsell. *J Neurosci* 1999)

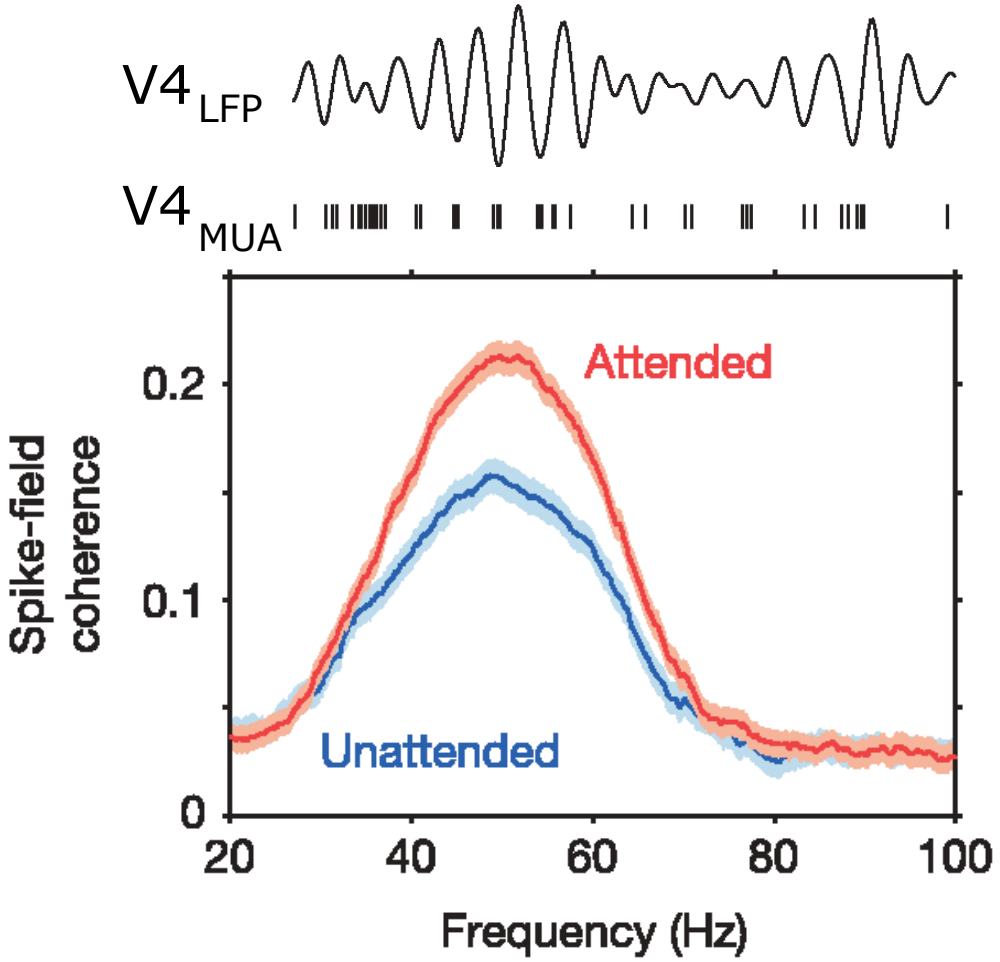
Enhancement of population profile selectivity





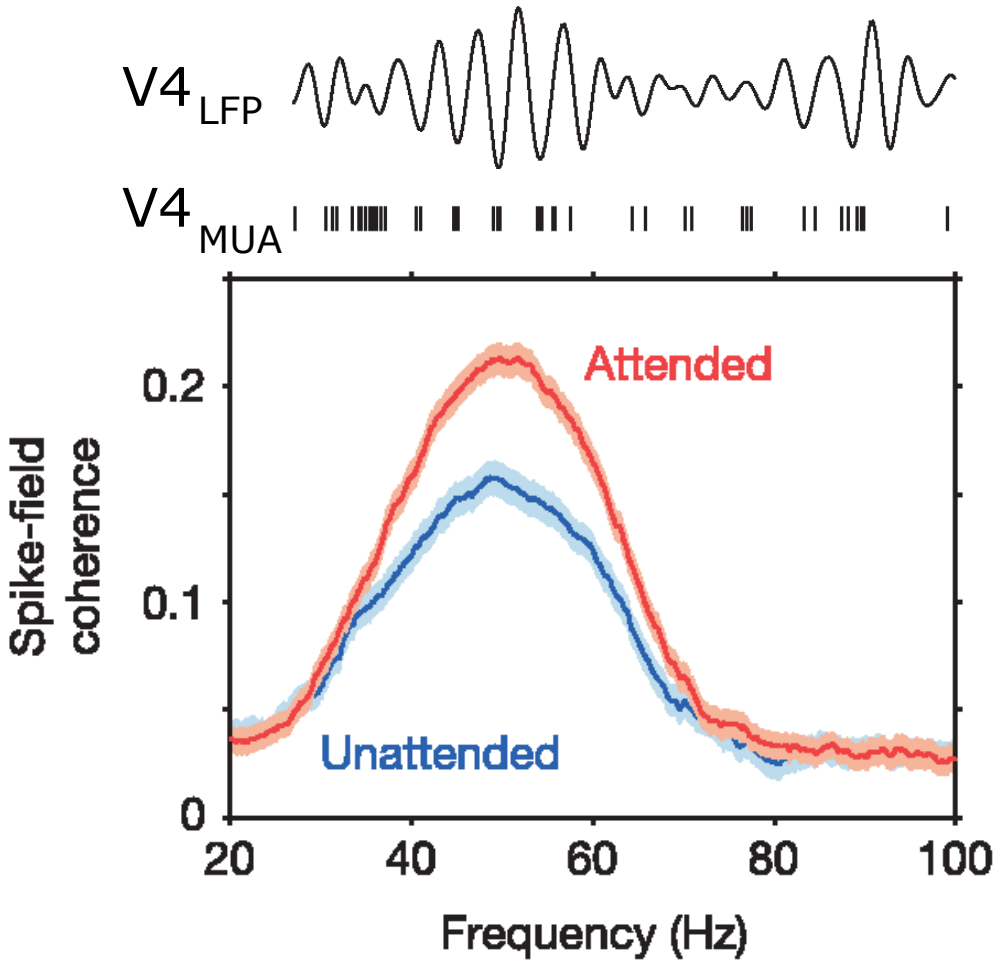
(Martínez-Trujillo and Treue, *Current Biology* 2004)

Attention increases synchrony in populations selective to attended object

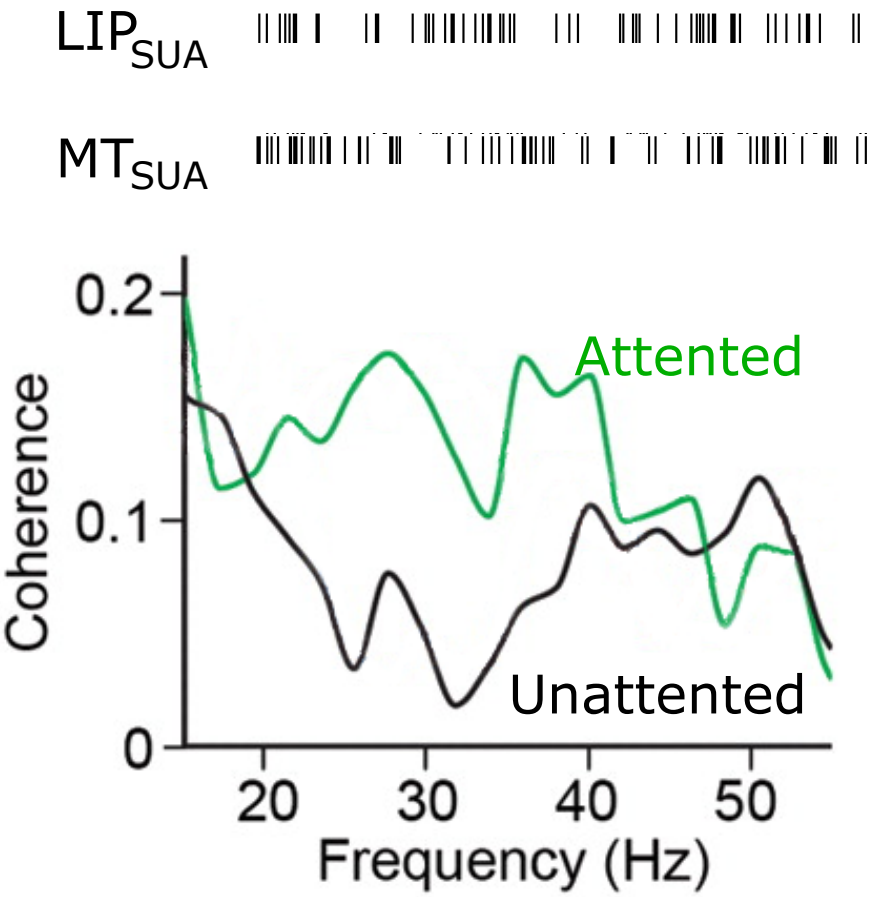


Womelsdorf et al., Nature 2006
Fries et al.. Science 2001

Attention increases synchrony in populations selective to attended object



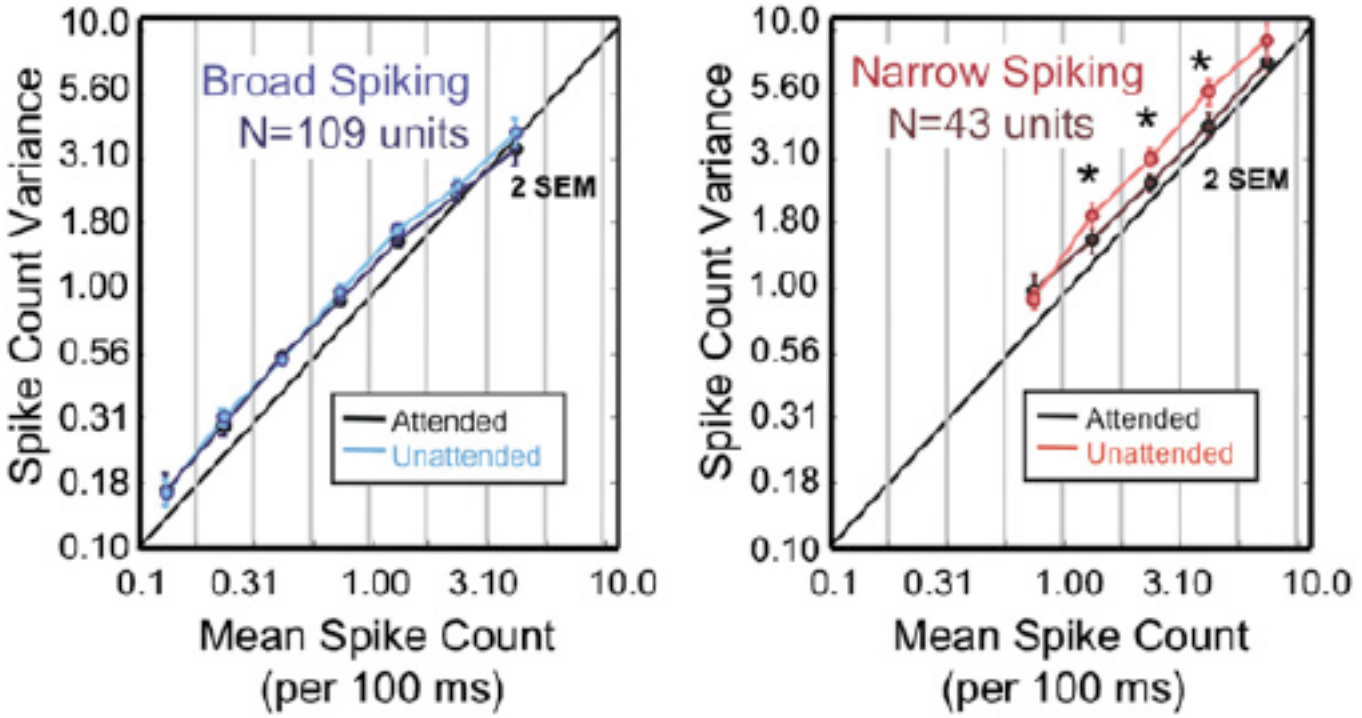
Womelsdorf et al., Nature 2006
Fries et al.. Science 2001



Saalmann et al., Science 2007

Fano factor remains ≃1 with selective attention

V4



Mitchell, Sundberg and Reynolds 2007

Different observations for different questions:

- What is the effect of attention on complex scenes? → Biased Competition
- How does attention affect a neuron's tuning curve? → Multiplicative scaling
- How does attention modulate the neural population response? → Selectivity enhancement
- What about the temporal dynamics of spiking? → Synchrony and oscillation enhancement, but little variability modulation

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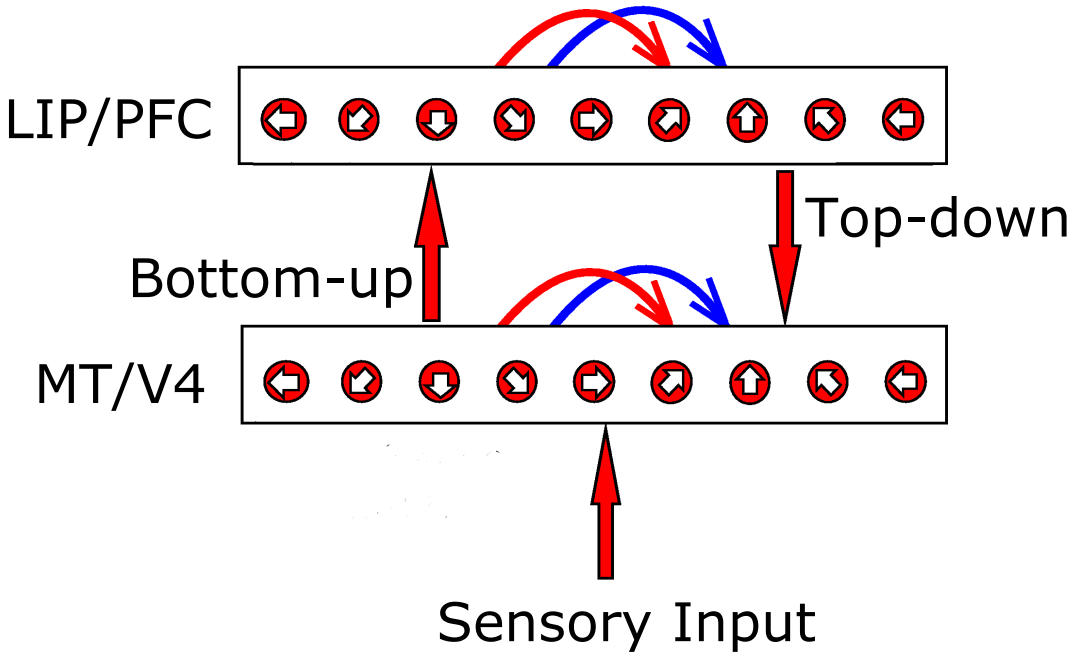
How can we integrate all this in a single computational framework? What are the mechanisms?

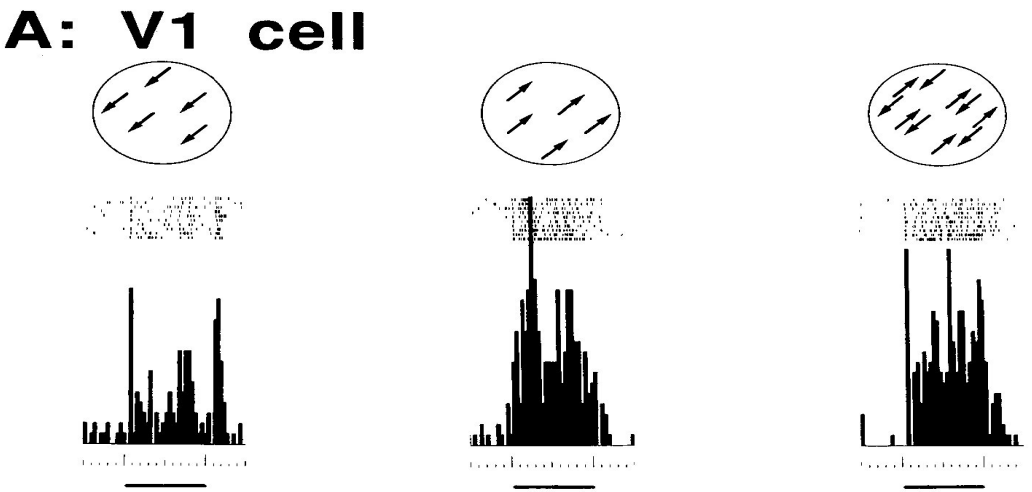
The network model

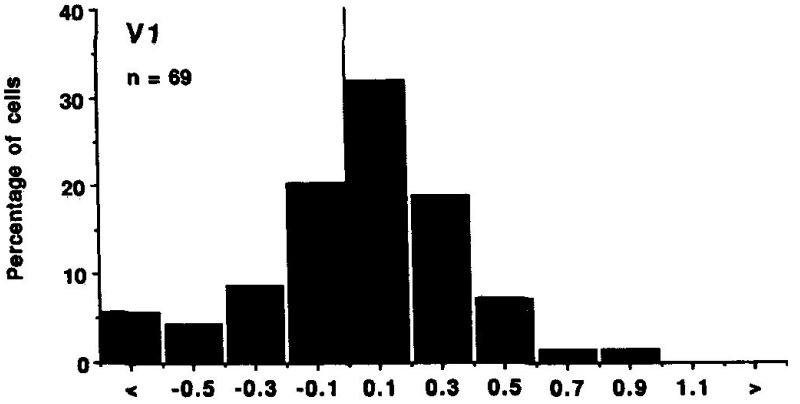


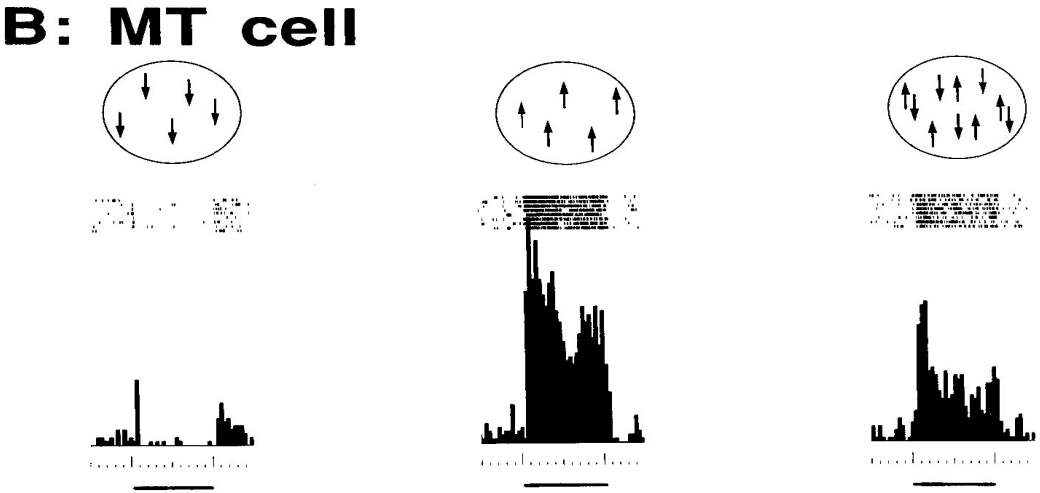
- MT neuronal responses and firing statistics compatible with experiments
- Integrates a persistent activity area (PFC/LIP) and a sensory area (MT/V4)
- Integrates the effects of feature-based attention on firing rates and synchrony

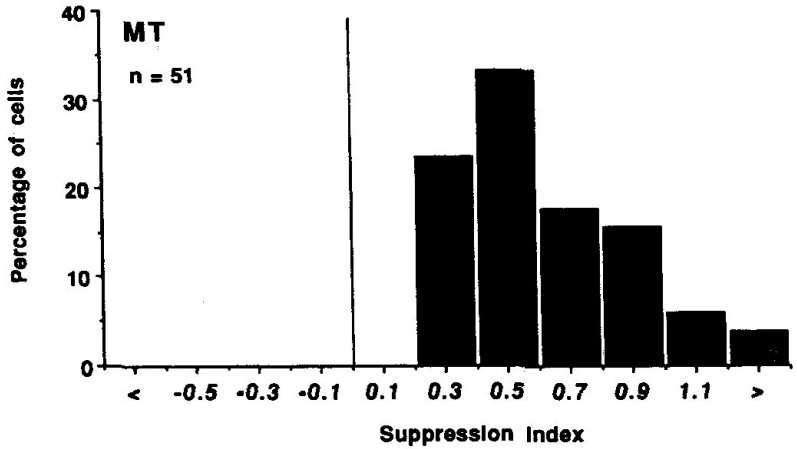
Ardid, Wang, Compte. J Neurosci 2007
Ardid, Wang, Gomez-Cabrero, Compte. J Neurosci 2010

V1 and MT responses to transparent motion stimulation



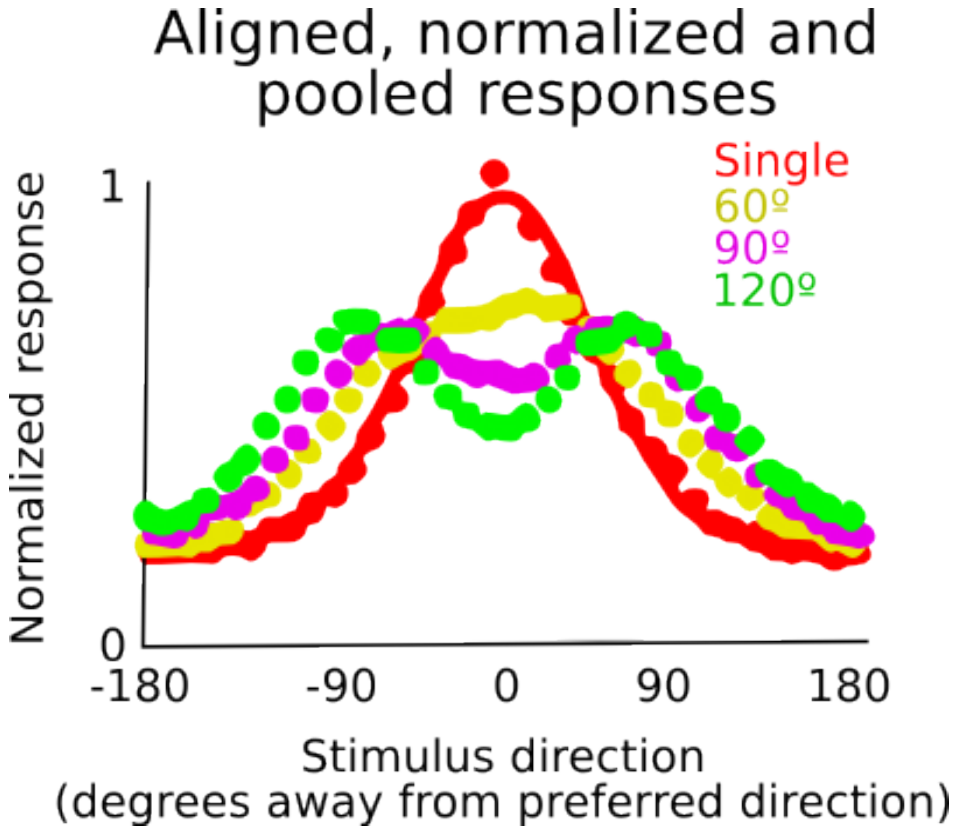






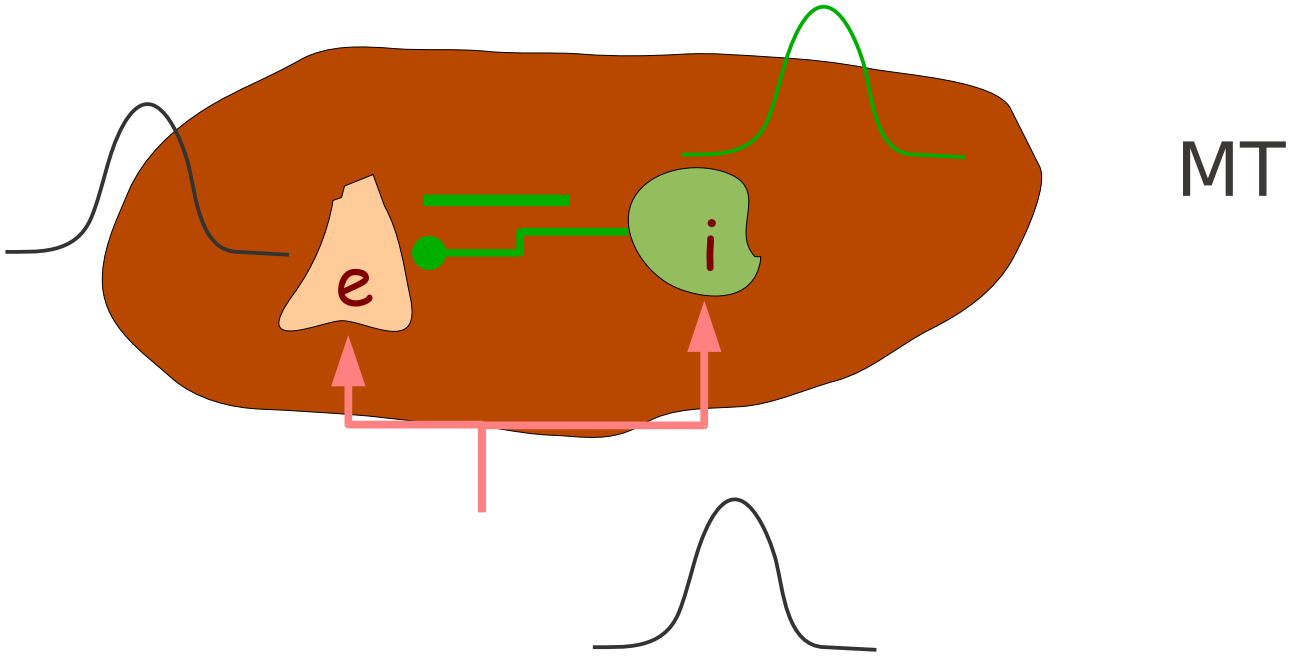
Snowden et al. 1991

MT responses to transparent motion stimulation

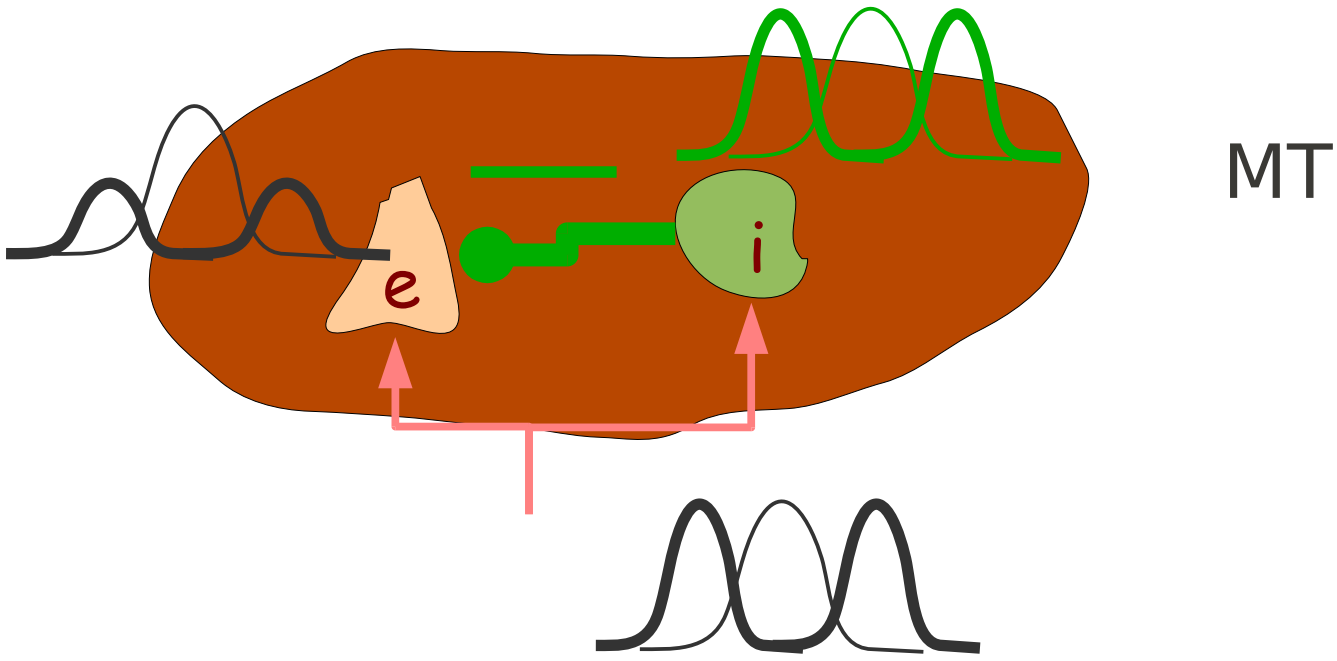


Treue et al. 2000

MT network: normalization by strong feedforward inhibition



MT network: normalization by strong feedforward inhibition



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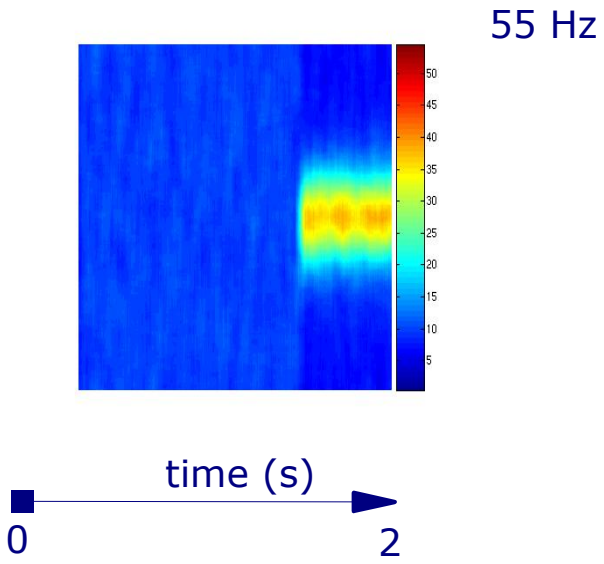
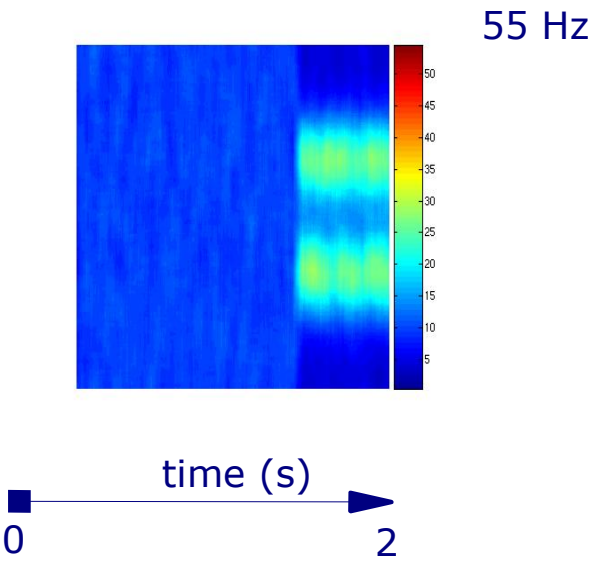
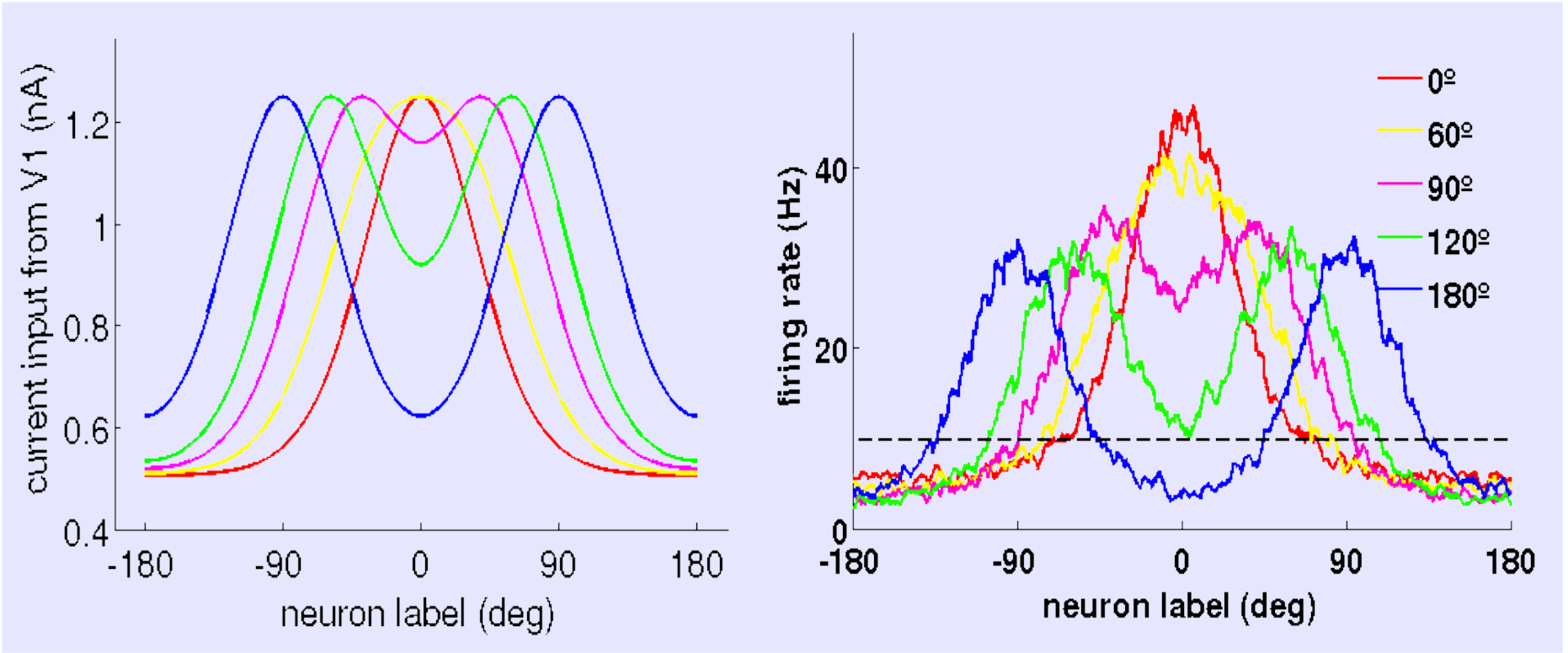




MT network: normalization by strong feedforward inhibition

Input coming from V1

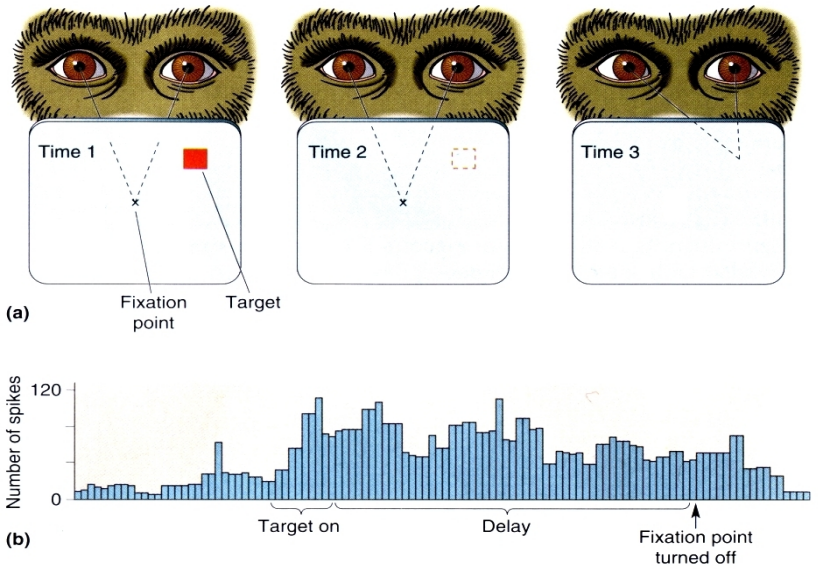
MT model output

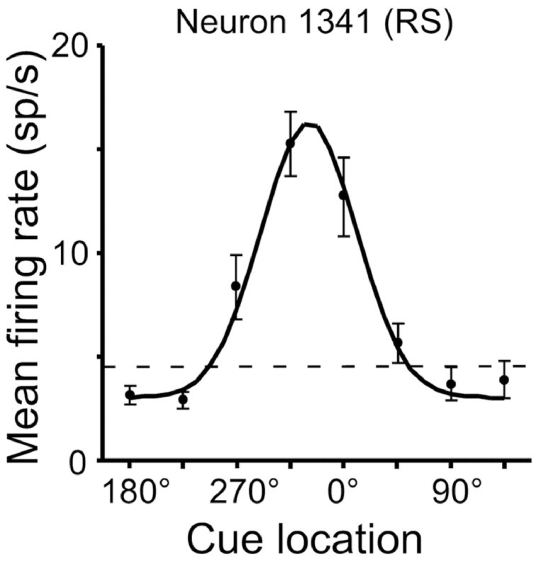


Snowden, Treue, Erickson, Andersen 1991; Heeger 1992; Treue et al., 2000

A persistent activity network as the source of attentional bias

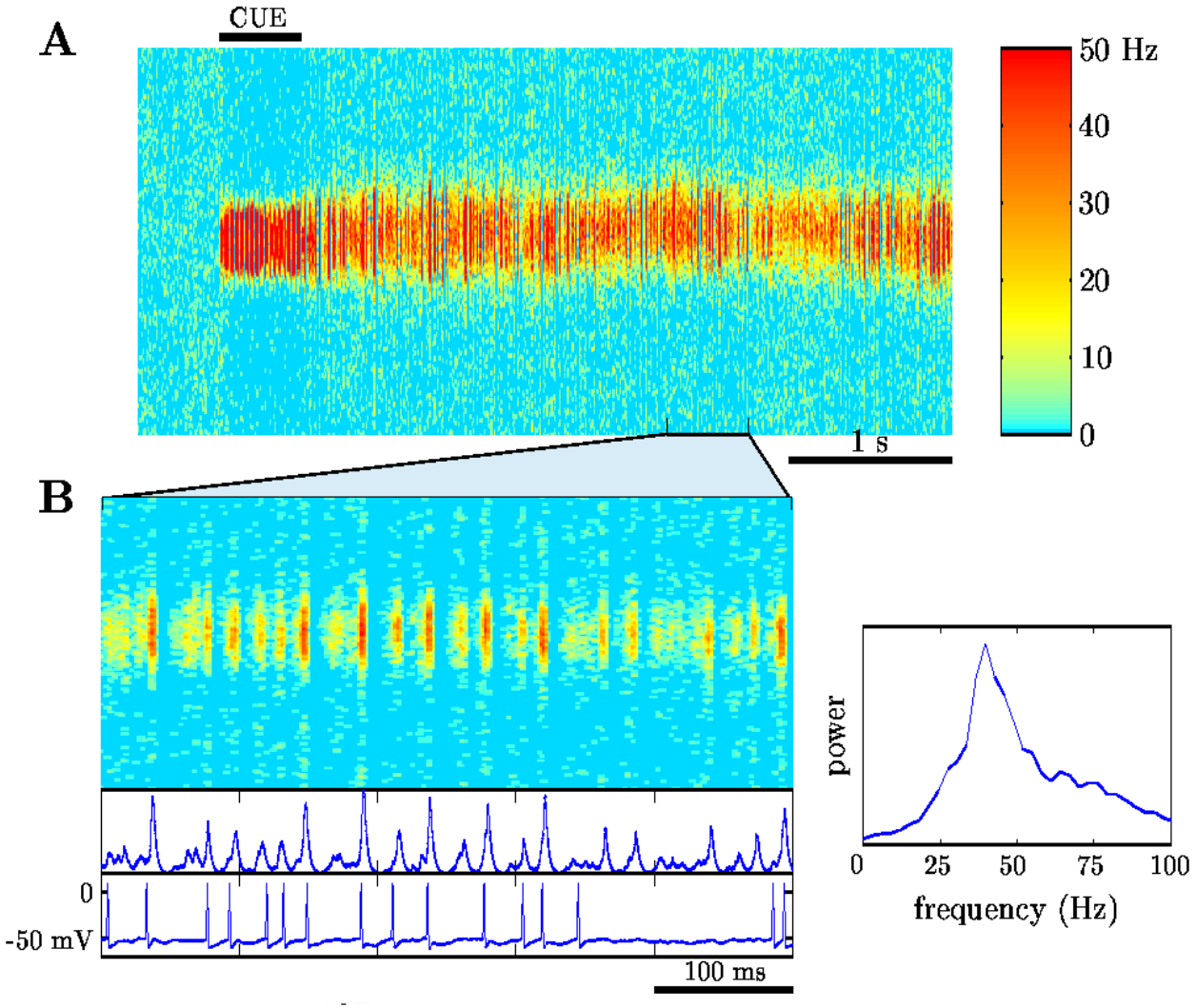
Desimone and Duncan. Ann. Rev. Neurosci. 1995





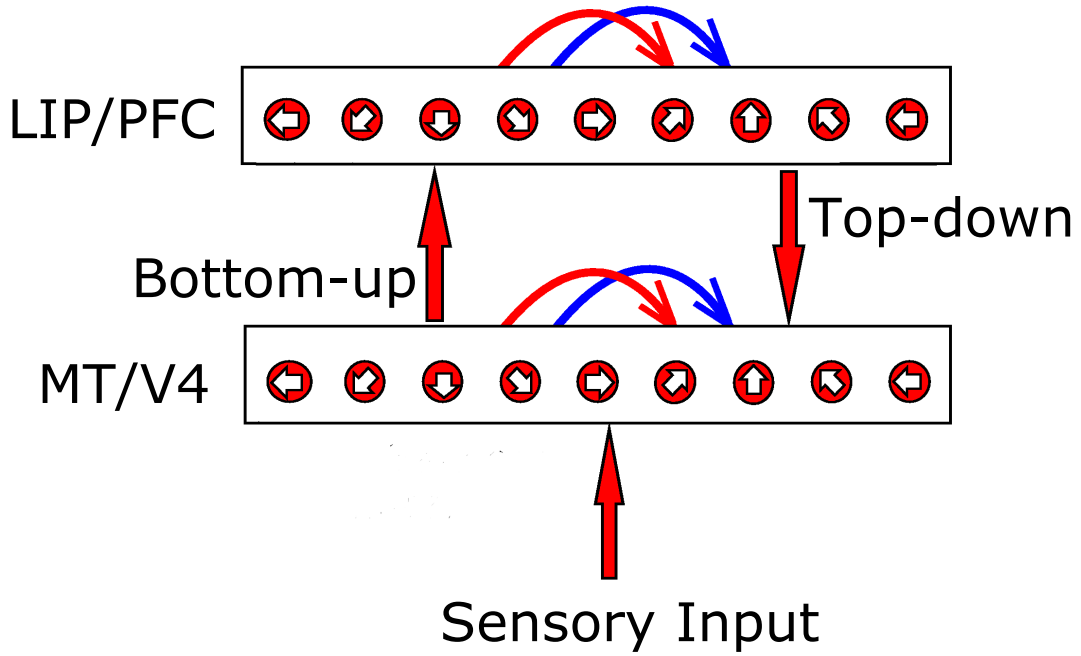
Gnadt and Andersen 1988; Funahashi et al. 1989; Goldman-Rakic 1995

Recurrent excitation and inhibition generate fast (40 Hz) coherent oscillations

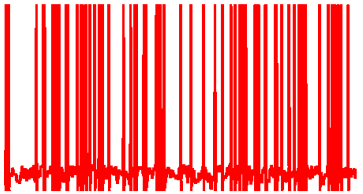


Compte, Brunel, Goldman-Rakic and Wang. Cereb Cortex 2000

The network model

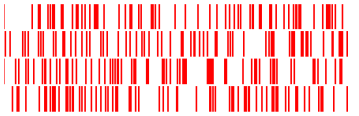


The network model

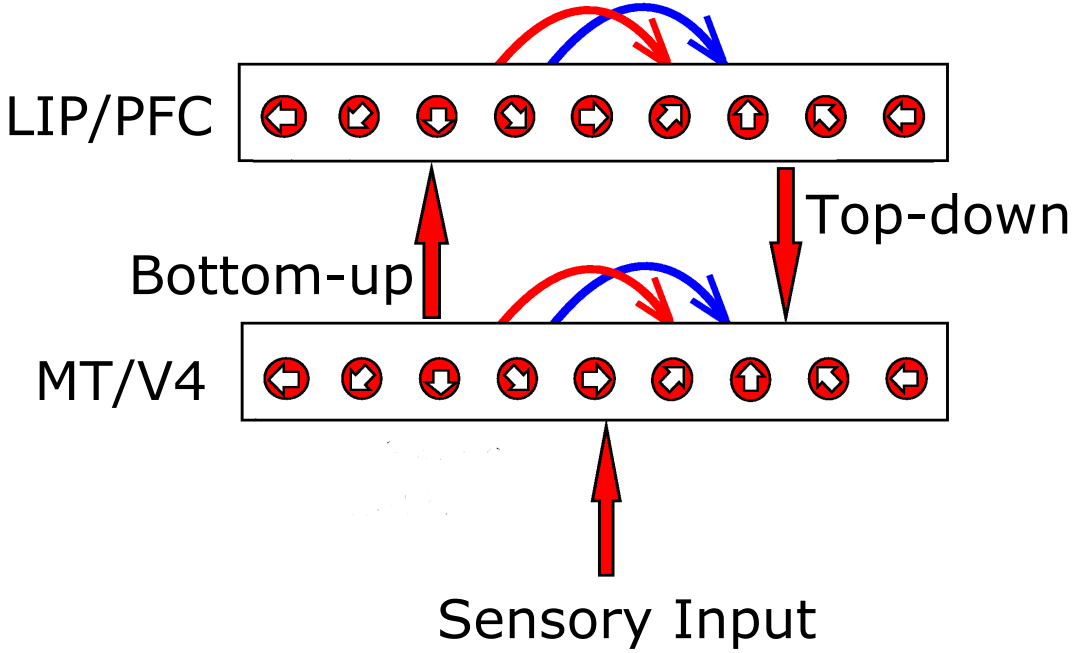


V_m

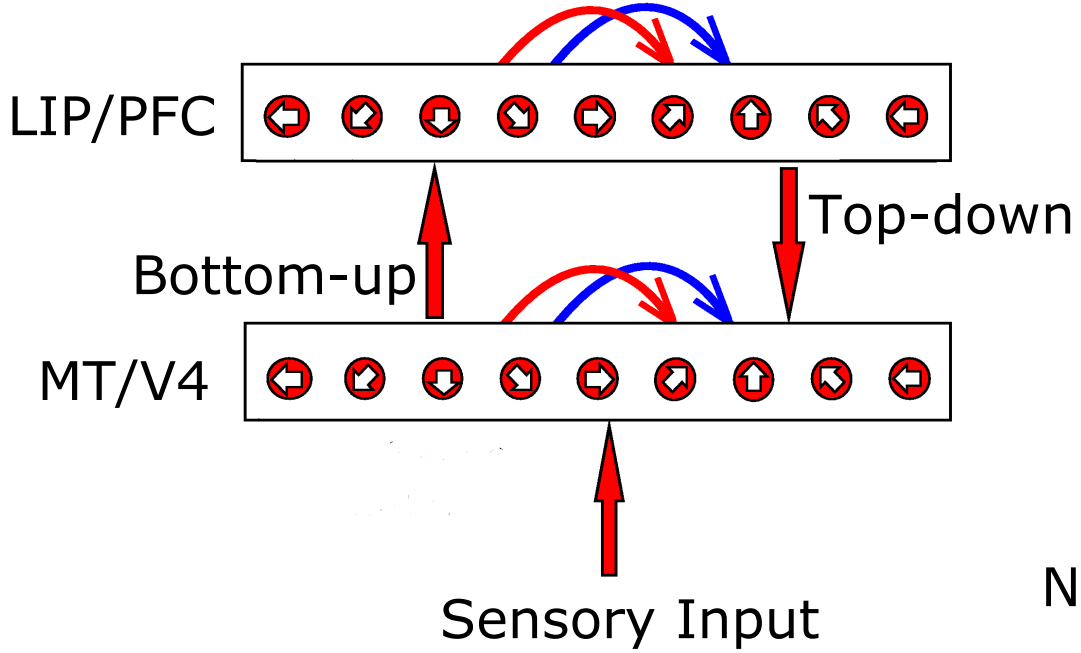
Neuron



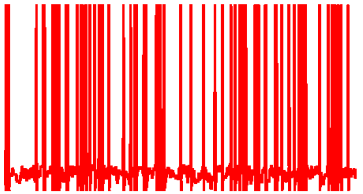
Spike trains



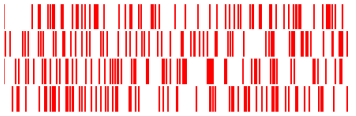
The network model



Neuron

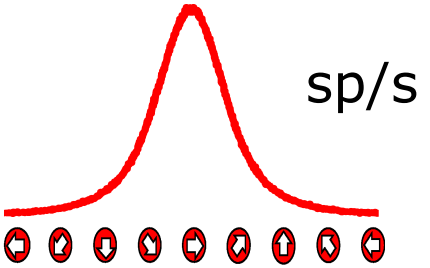


V_m

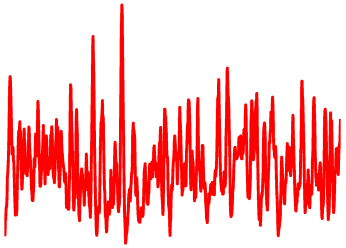


Spike trains

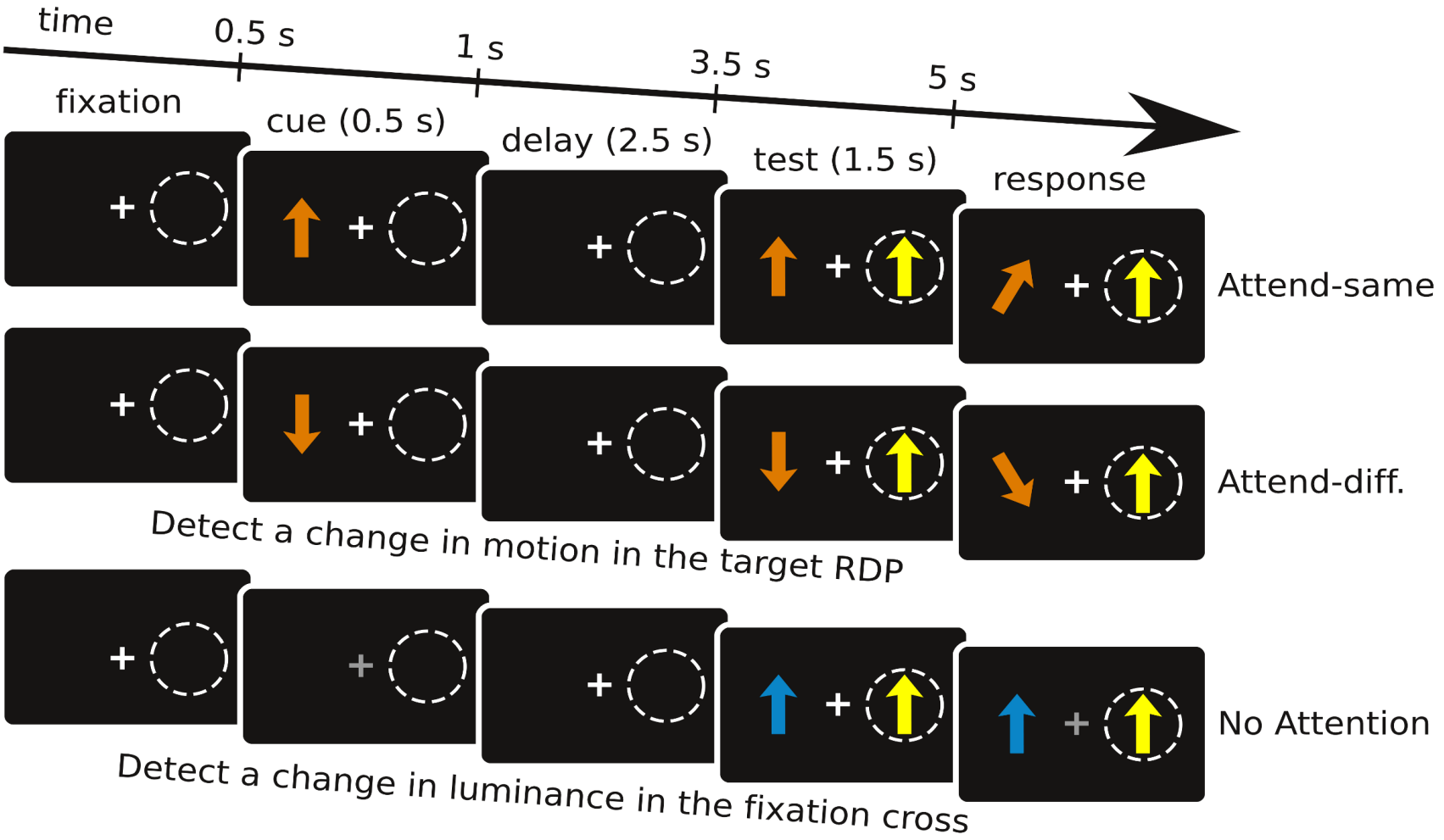
Network

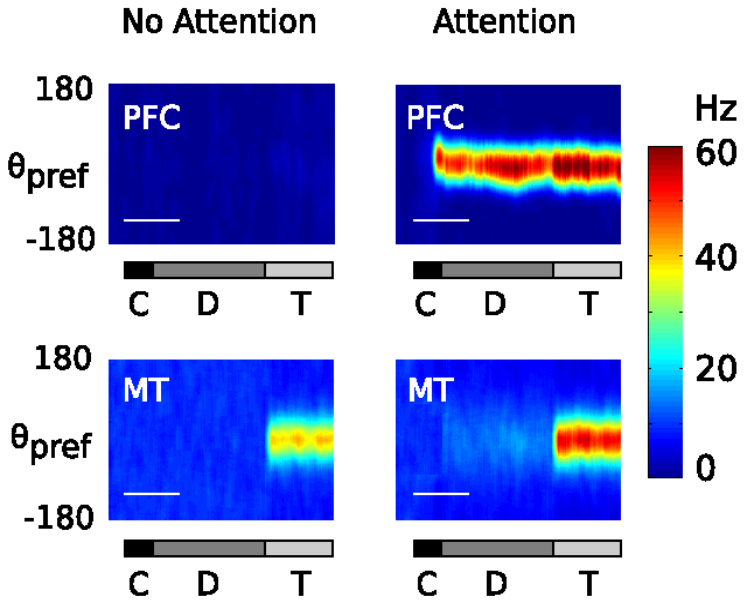


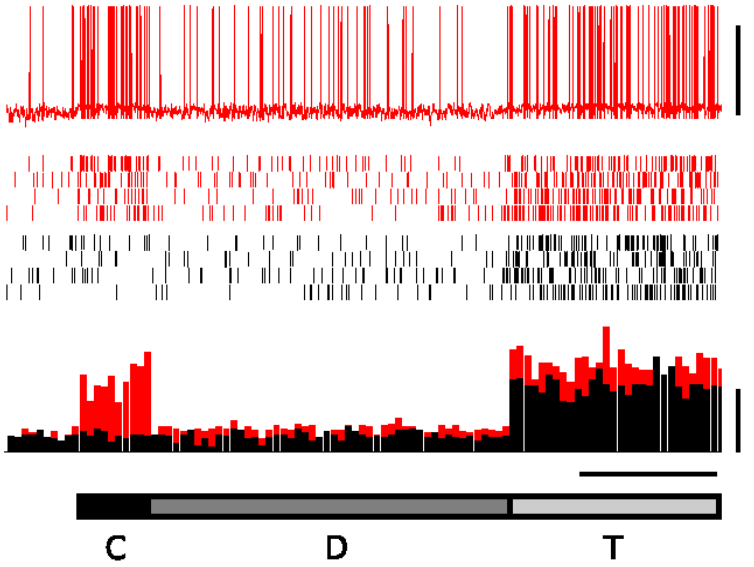
Population profile

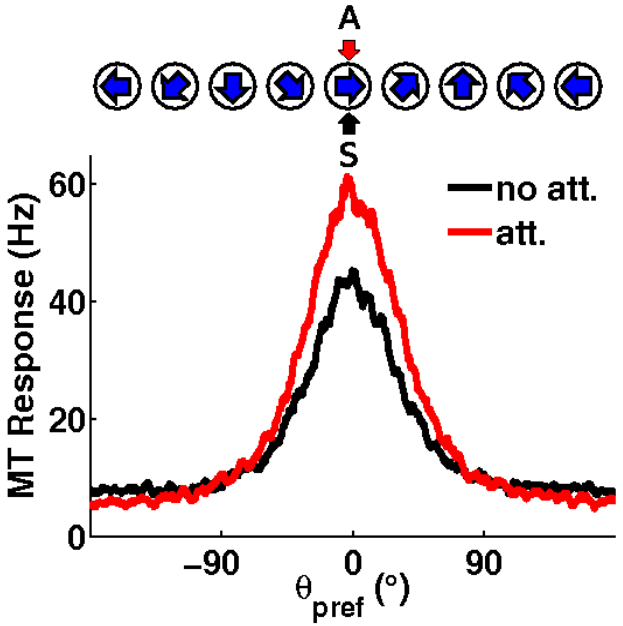


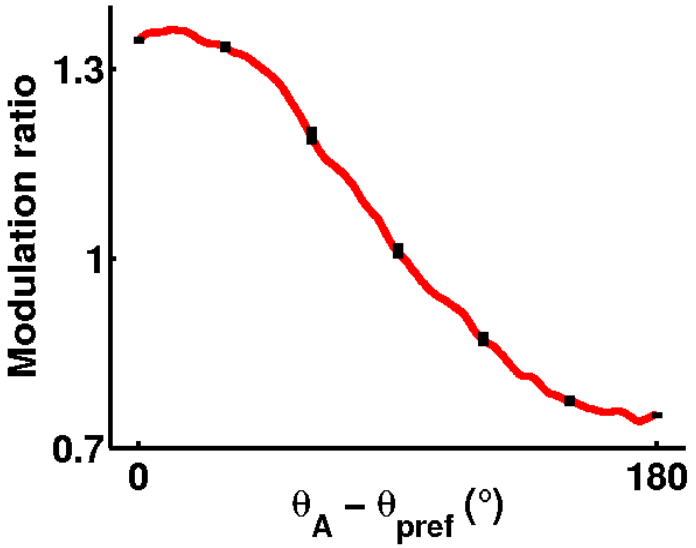
LFP

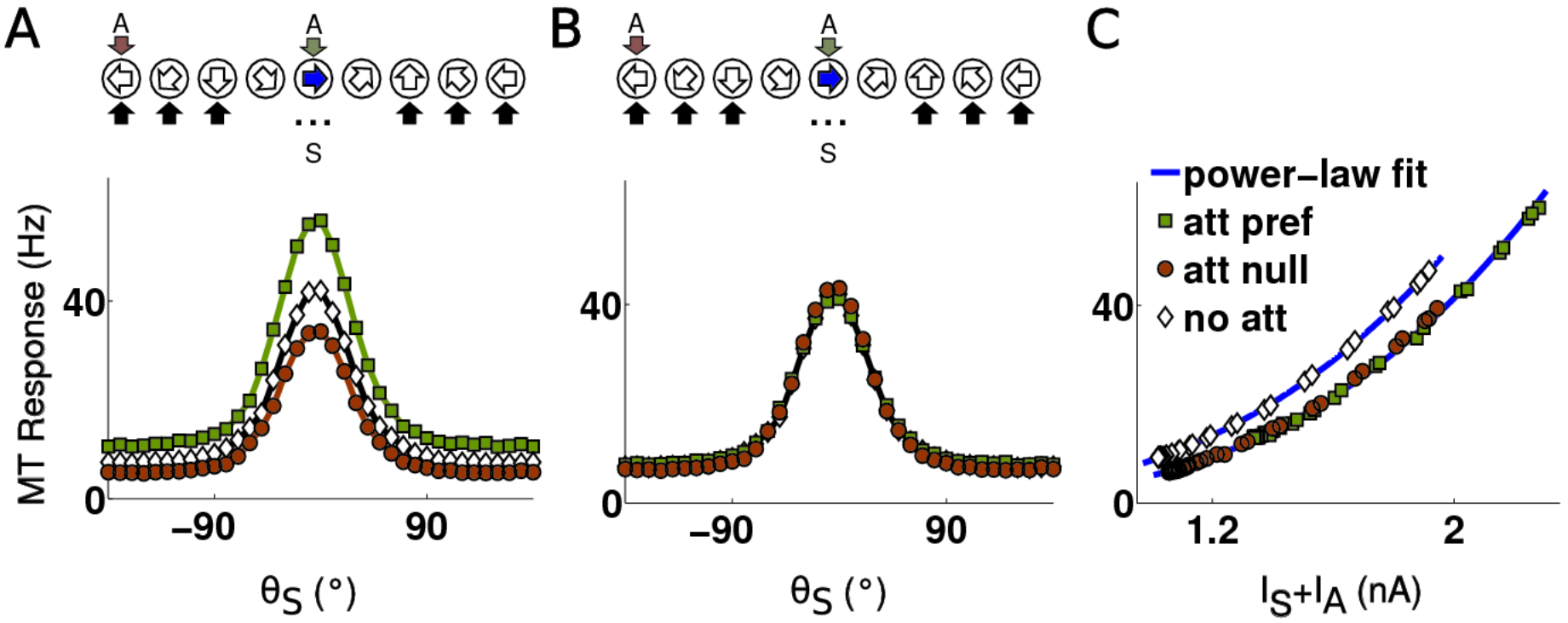

time
0.5 s
1 s
3.5 s
5 s
fixation
cue (0.5 s)
delay (2.5 s)
test (1.5 s)
response
Attend-same
Attend-diff.
Detect a change in motion in the target RDP
No Attention
Detect a change in luminance in the fixation cross


No Attention
Attention
180
θpref
-180
PFC
PFC
MT
MT
C
D
T
Hz
60
40
20
0


C
D
T

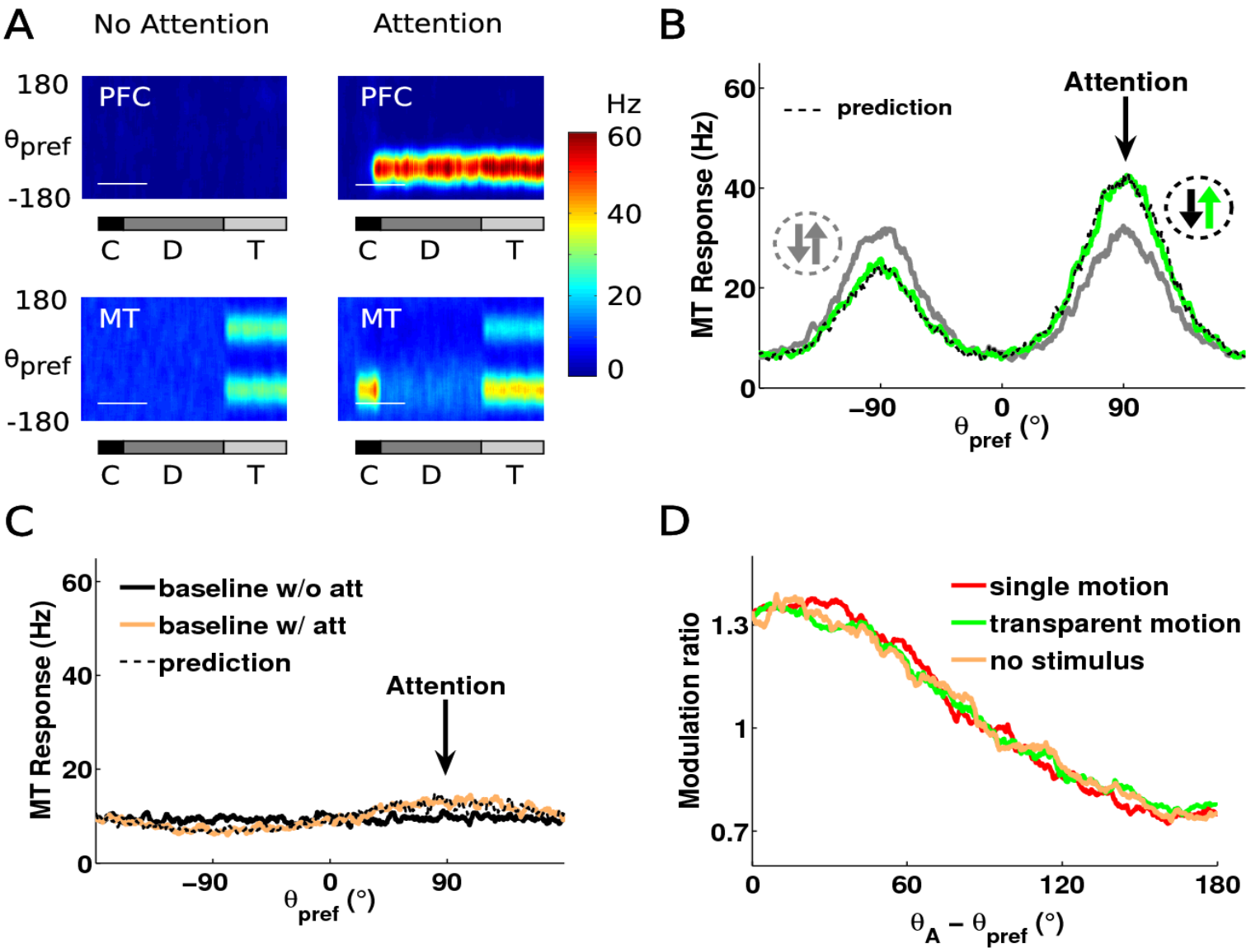

A
S
no att.
att.
MT Response (Hz)
60
40
20
0
−90
0
90
θpref (°)


Modulation ratio
1.3
1
0.7
0
180
θA − θpref (°)



Murphy and Miller, 2003

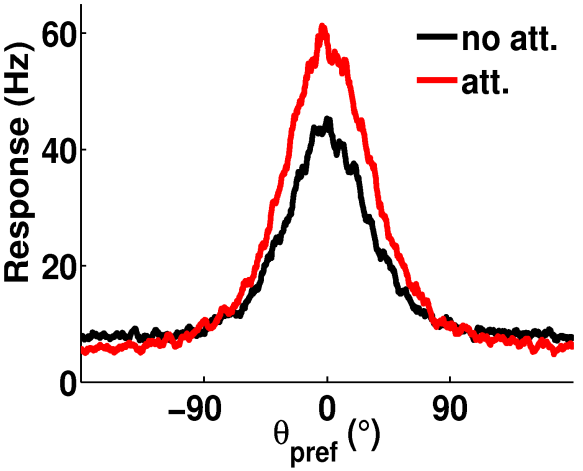
Feature-similarity gain model



The network model produces:

Selectivity enhancement

Martinez-Trujillo & Treue, Curr Biol 2004



Ardid et al., J Neurosci 2007

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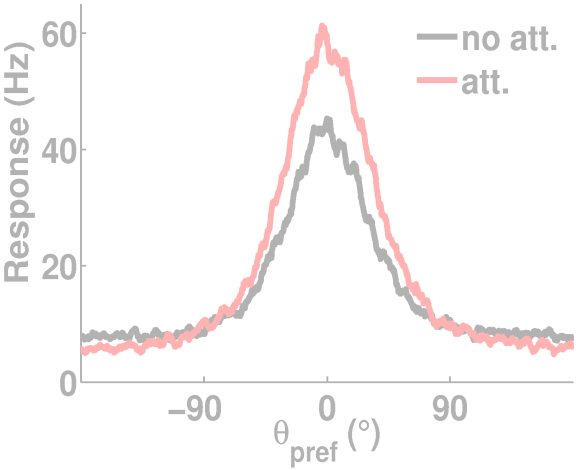
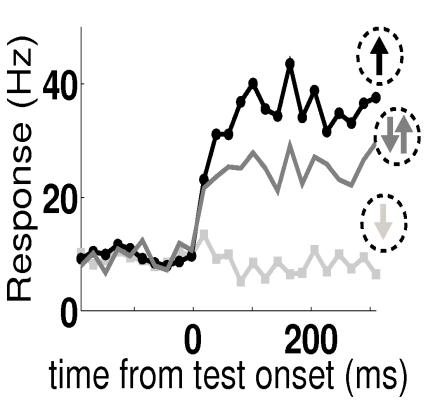
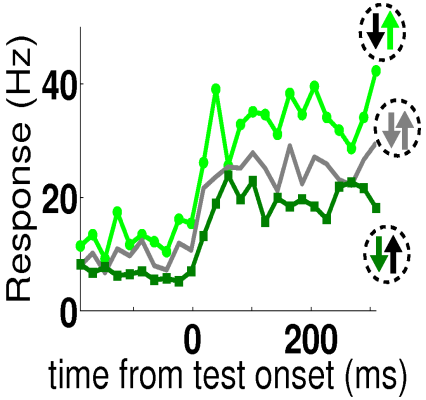
Martinez-Trujillo & Treue, Curr Biol 2004







Biased Competition

Moran & Desimone, Science 1985

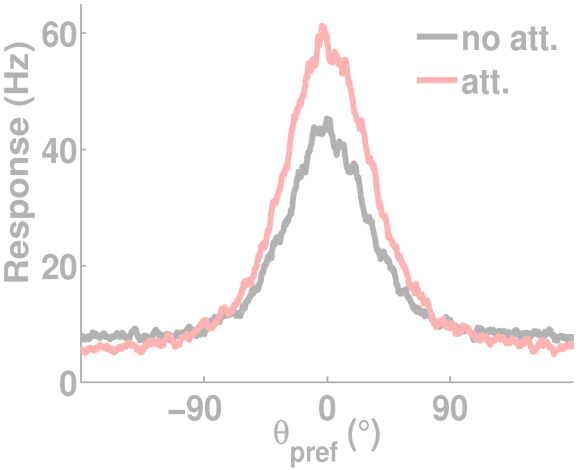
Treue & Maunsell, Nature 1996

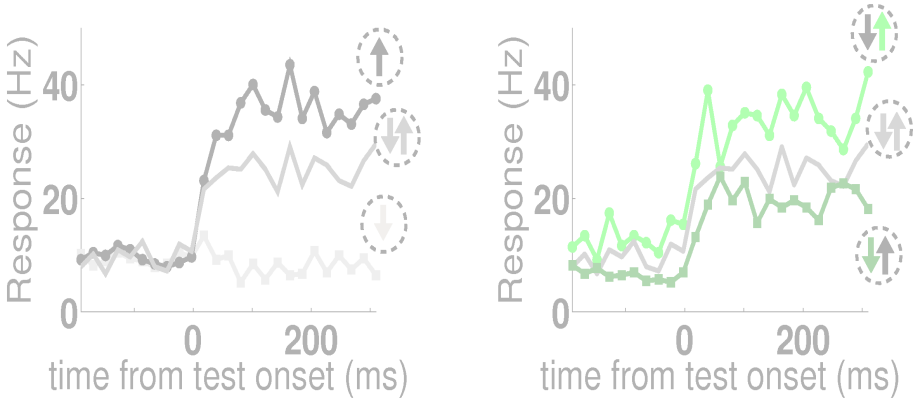
Ardid et al., J Neurosci 2007

The network model produces:

Selectivity enhancement

Martinez-Trujillo & Treue, Curr Biol 2004





Biased Competition

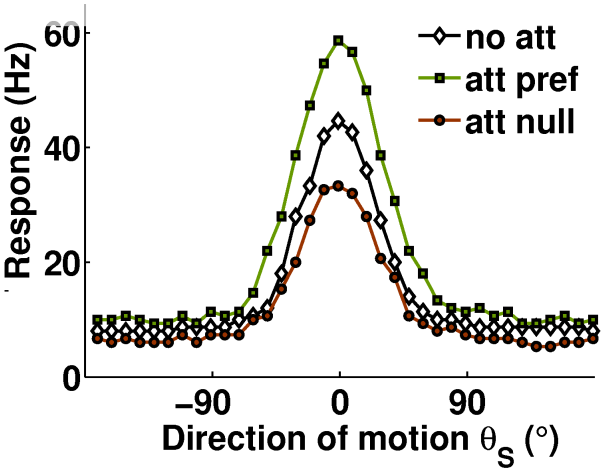
Moran & Desimone, Science 1985

Treue & Maunsell, Nature 1996

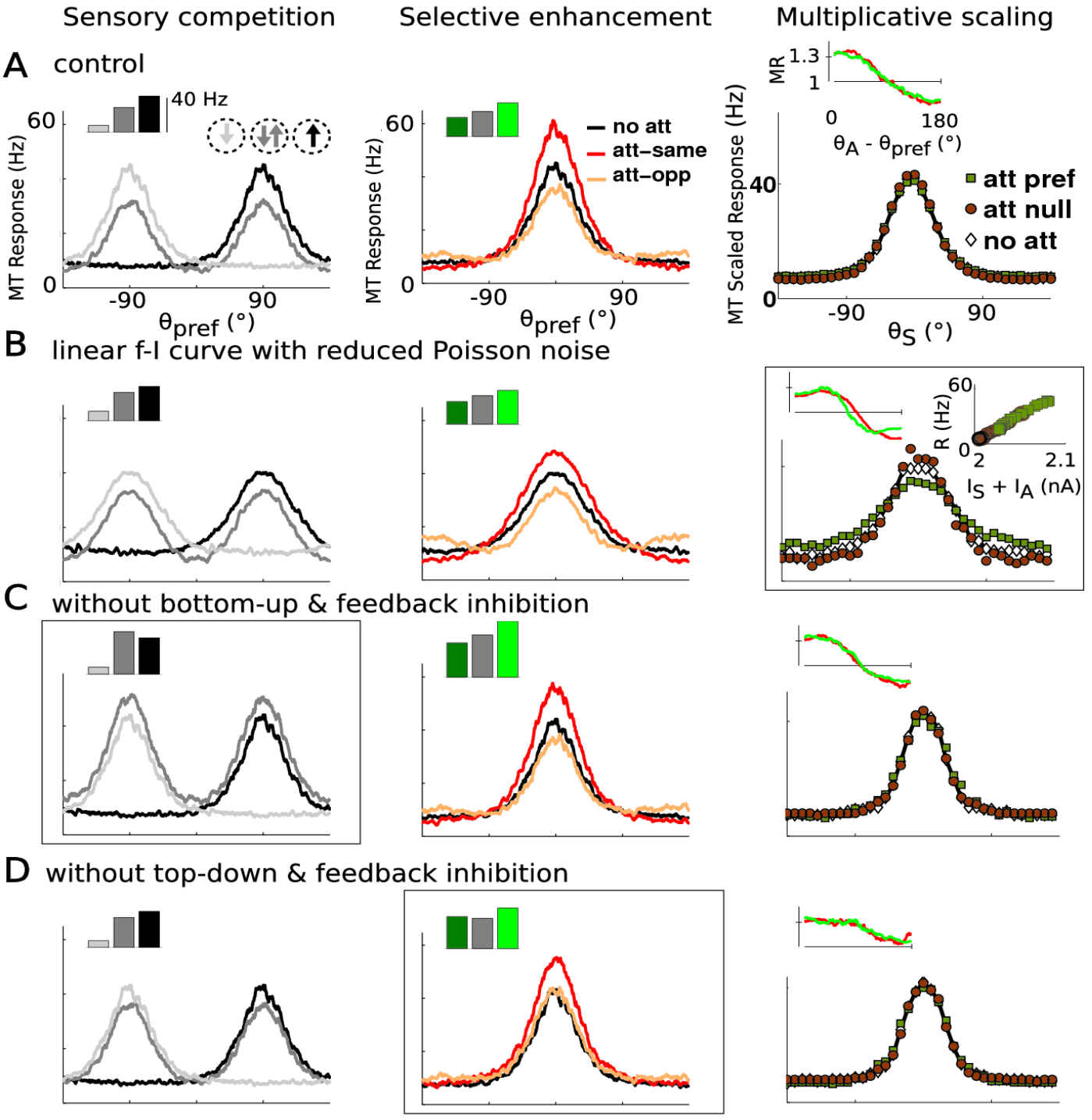
Multiplicative effect

McAdams & Maunsell, J Neurosci 1999

Treue & Martinez-Trujillo, Nature 1999



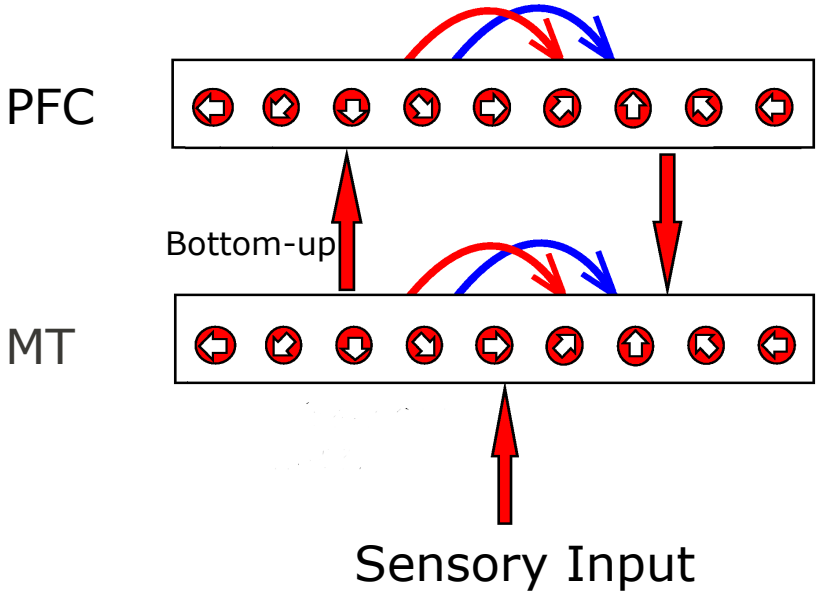
Ardid et al., J Neurosci 2007

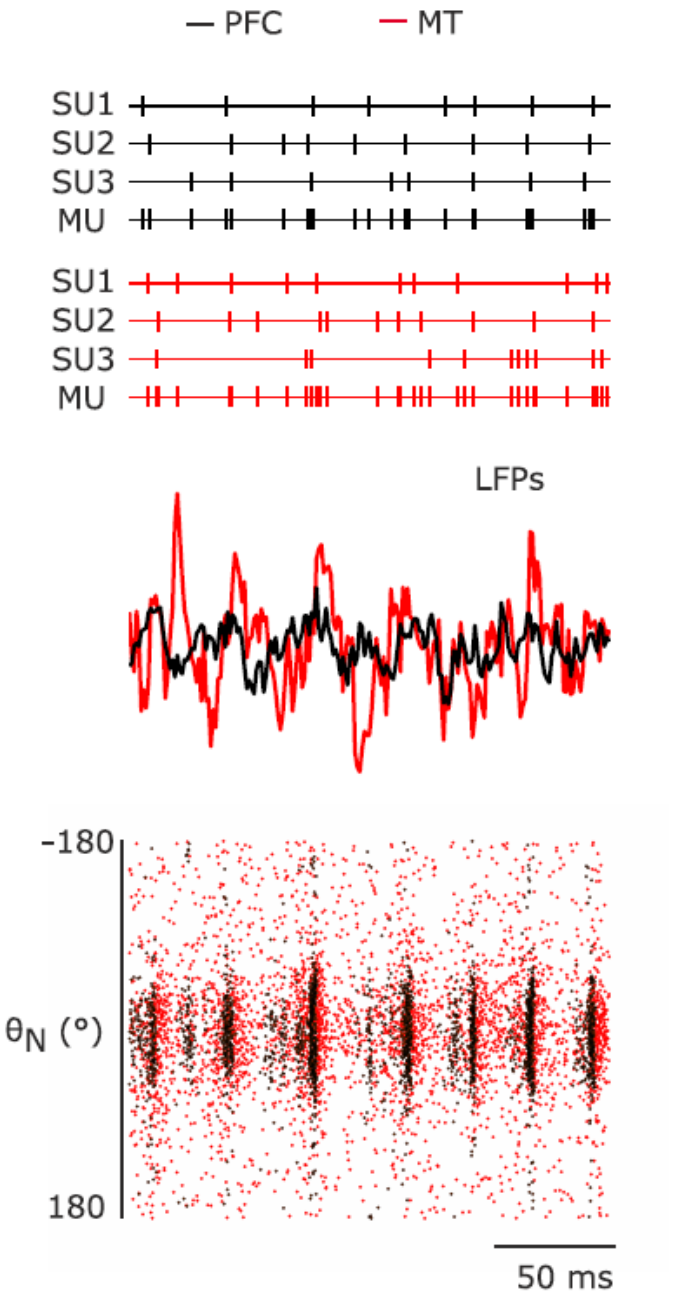

Sensory competition
Selective enhancement
Multiplicative scaling
A control
40 Hz
60
0
MT Response (Hz)
-90
90
θpref (°)
no att
att–same
att–opp
MR
1.3
1
0
180
θA - θpref (°)
MT Scaled Response (Hz)
40
att pref
att null
no att
θS (°)
B linear f-I curve with reduced Poisson noise
R (Hz)
2
2.1
IS + IA (nA)
C without bottom-up & feedback inhibition
D without top-down & feedback inhibition

Conclusions 1

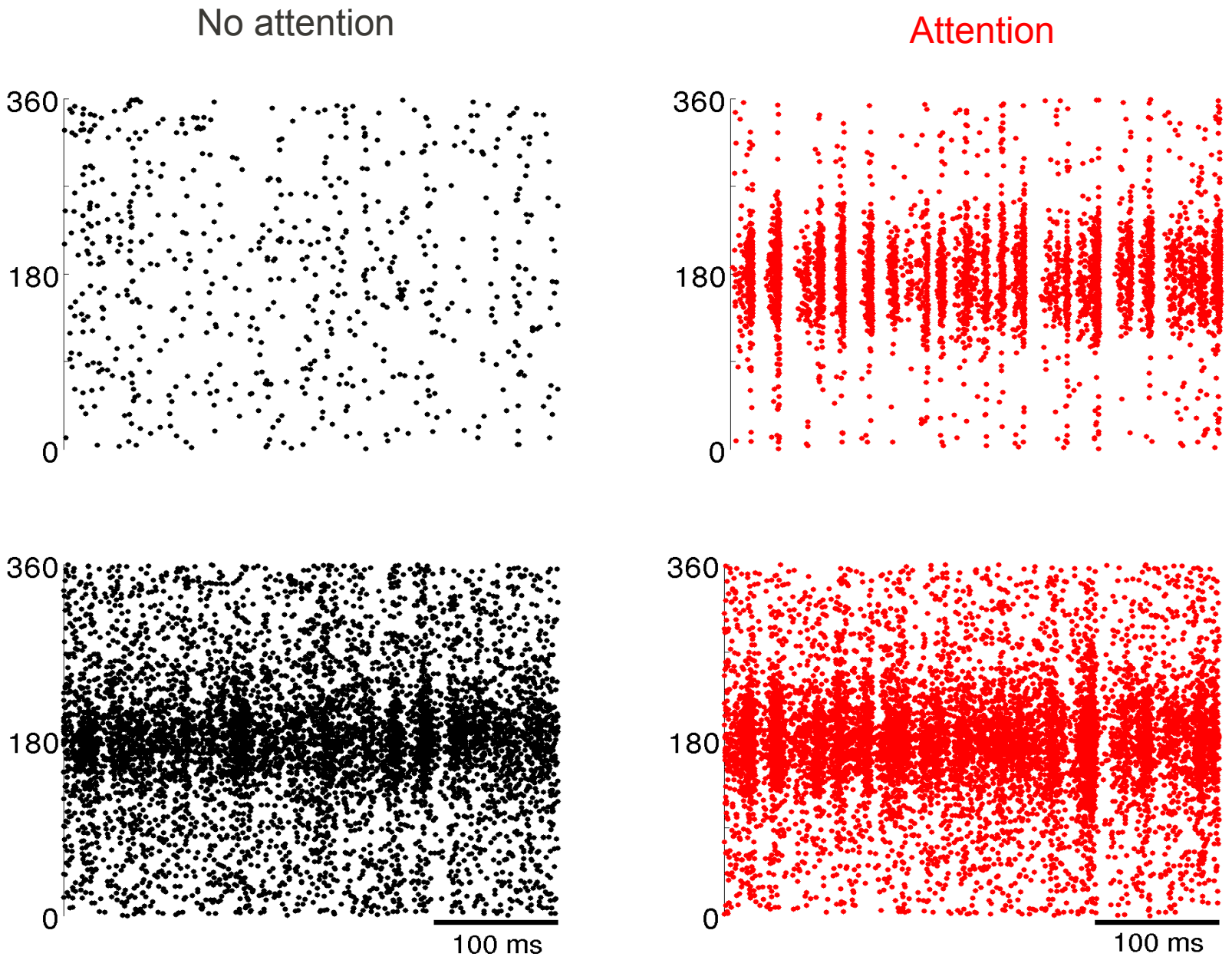
- Many neurophysiological correlates of selective attention can be understood coherently in a circuit model of two integrated cortical networks
- We identify a biologically plausible implementation of the FSGP, hitherto formulated on purely algorithmic terms.
- Essential mechanisms in MT:
  - strong feedforward inhibition from V1
  - top-down to excitatory *and* inhibitory neurons
  - non-selective intracortical inhibition
  - noisy bath generates power-law input-output

synchrony?

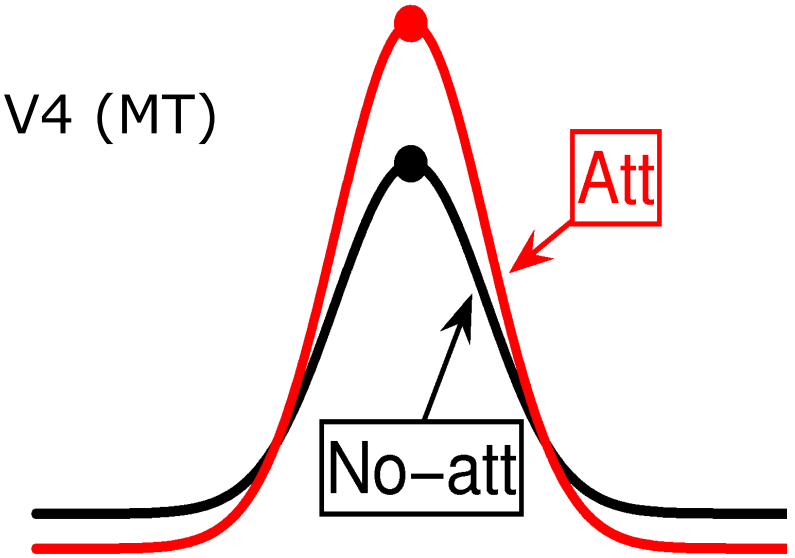




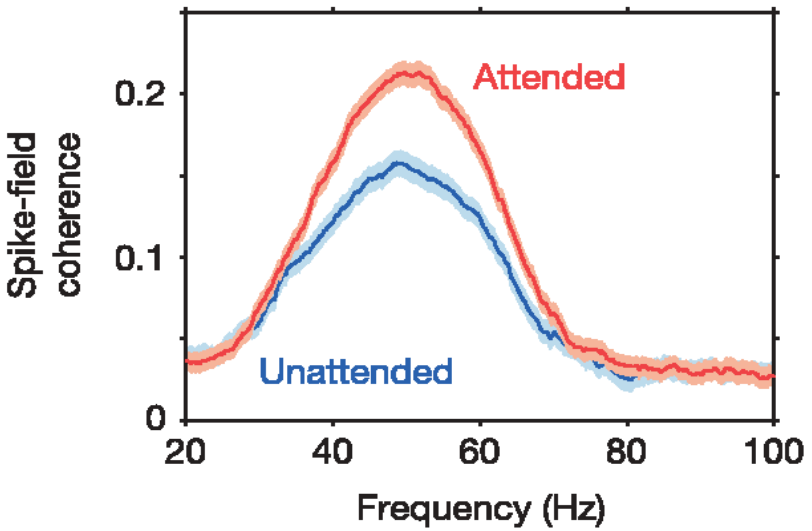
Ardid et al., J Neurosci 2010


No attention
Attention
360
180
0
360
180
0
360
180
0
100 ms
360
180
0
100 ms

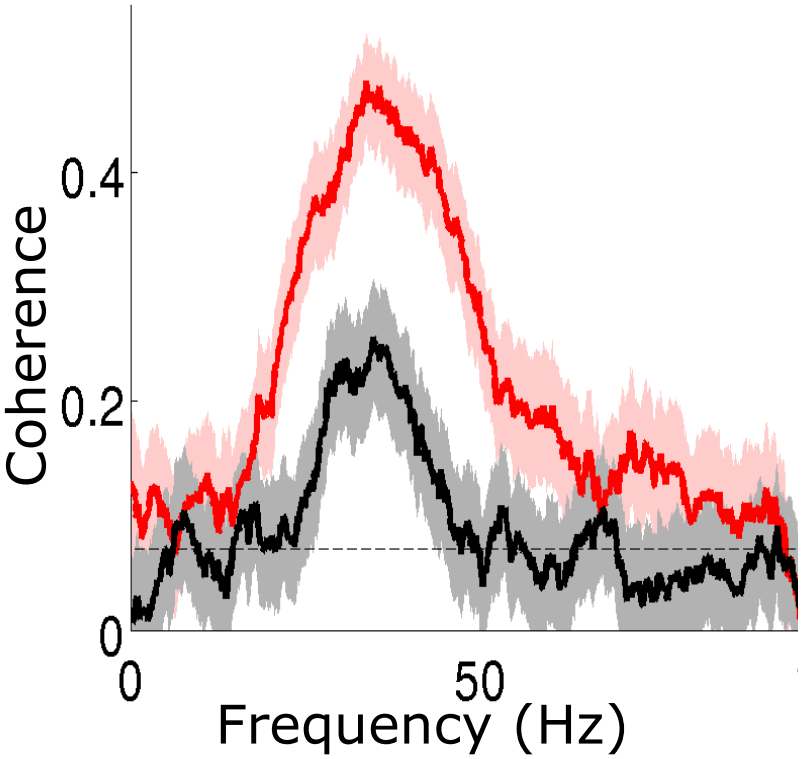
Local coherence (LFP-SUA)



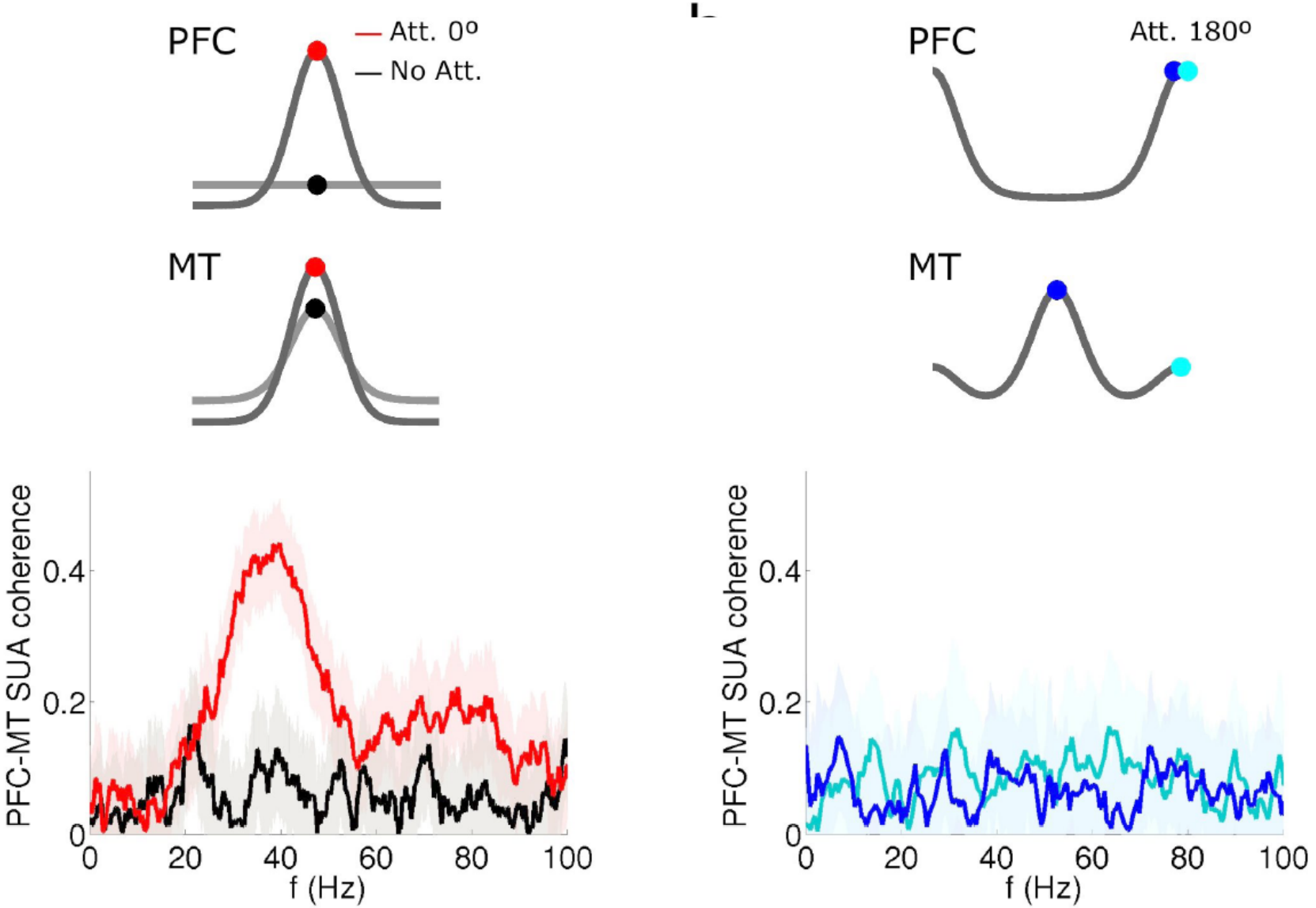
Experimental observation



Womelsdorf et al., Nature 2006

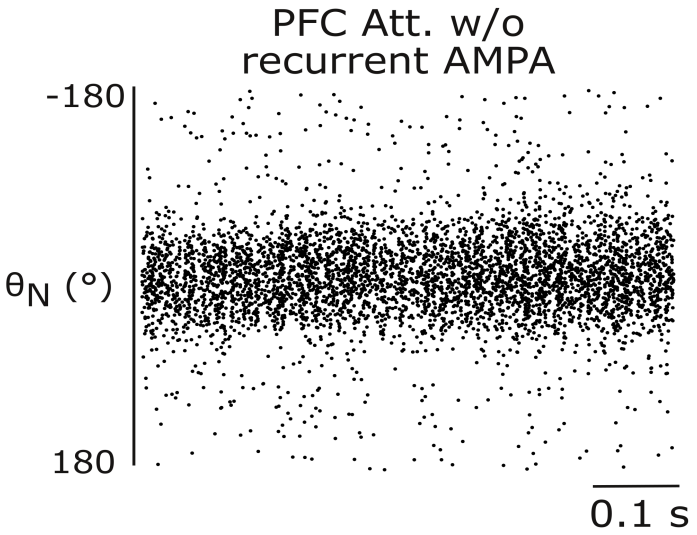


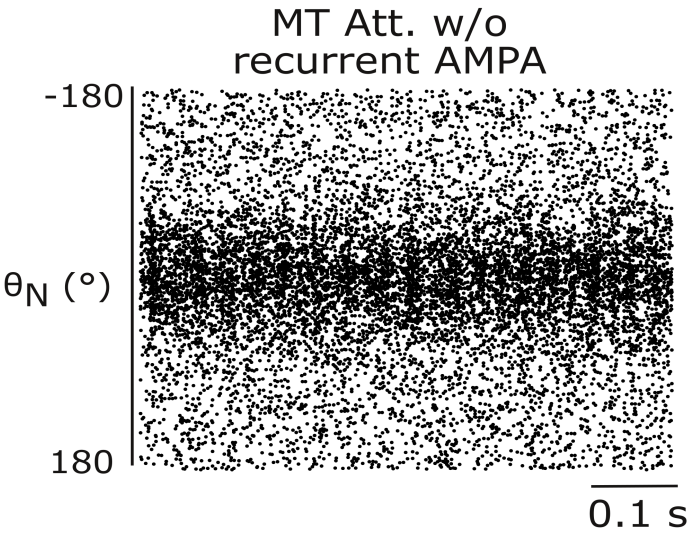
Inter-area coherence (SUA-SUA)

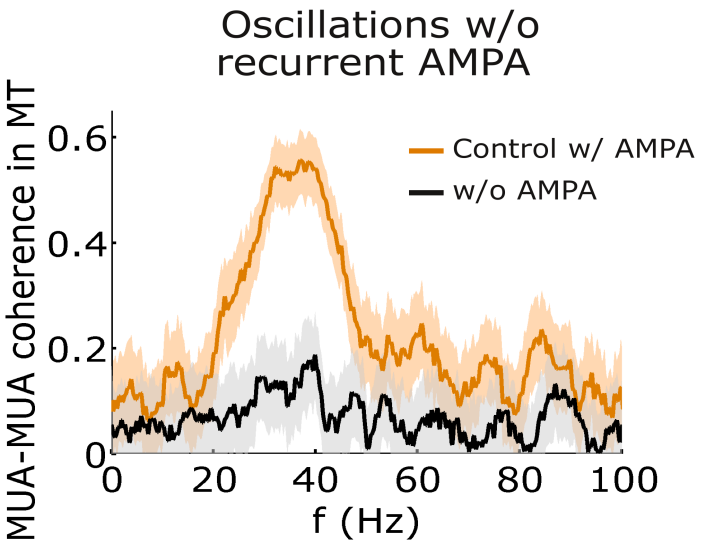


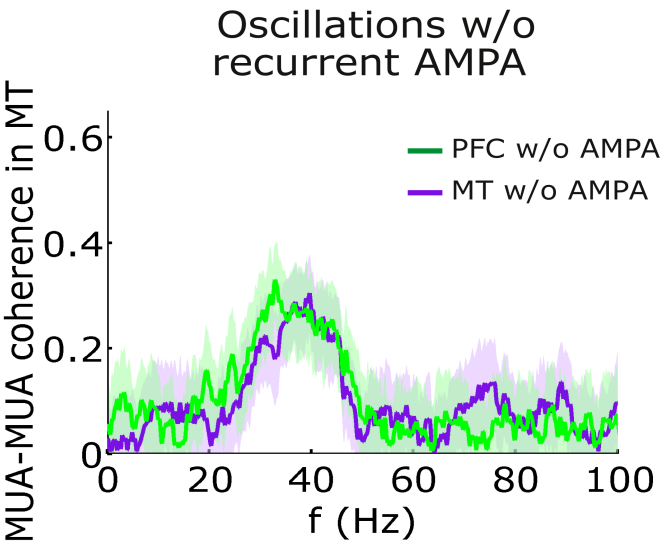
Communication through coherence?

Oscillations and synchronization require fast recurrent excitation in MT

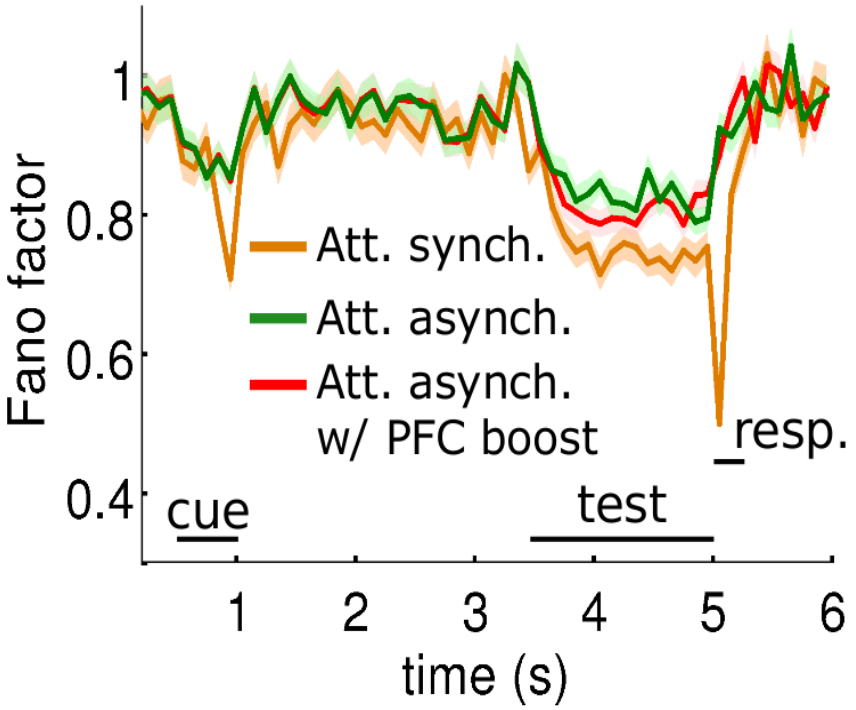


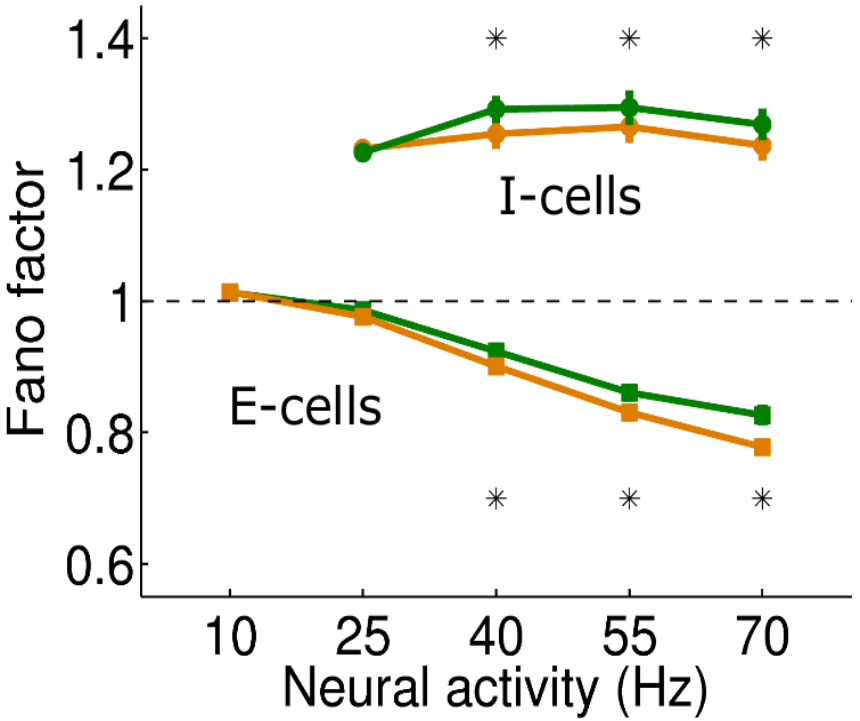






Spiking activity is highly irregular and shows little attentional modulation





cf Mitchell, Sundberg and Reynolds 2007

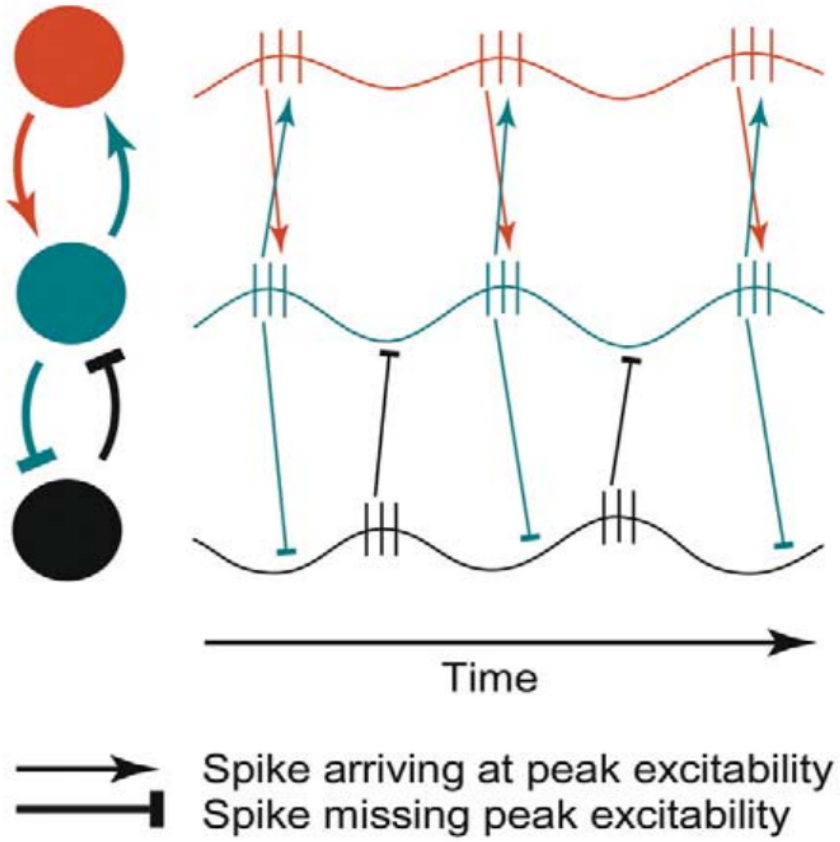
in agreement with experiments:

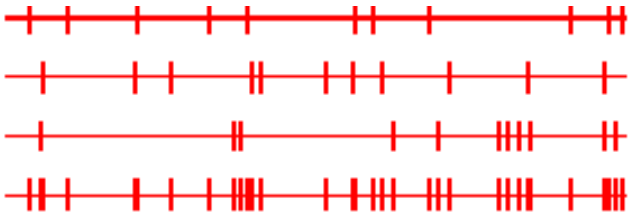
- synchrony between the two areas is only observed in attention trials, and in a selective way (prediction)
- the sensory network presents some degree of local synchrony, which augments with attention
- individual spike trains do not change statistics appreciably

Strong attentional modulations of synchrony can be reconciled with non-modulation of irregular spiking in a biophysical network module of e- and i-cells

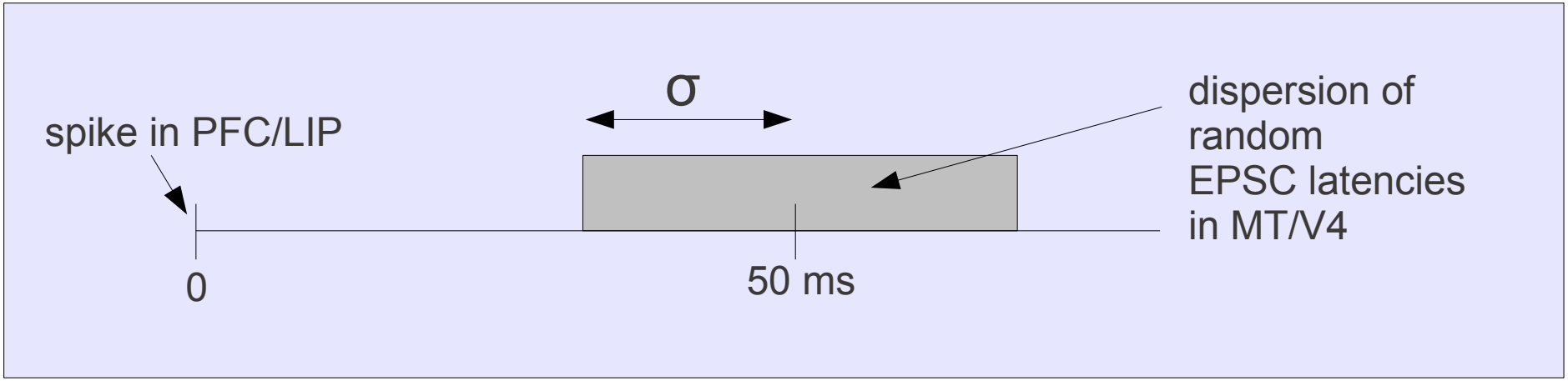
Does this have any functional effect in rate coding in MT?

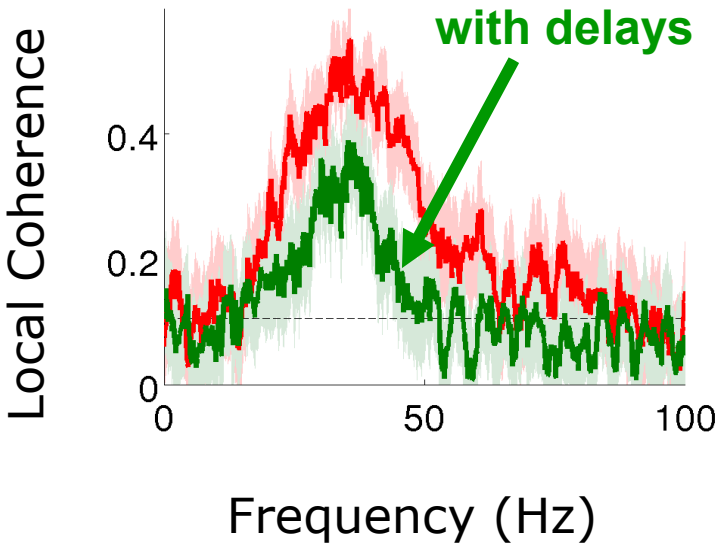
Synchronization routes information by enhancing downstream impact: the *communication through coherence* hypothesis

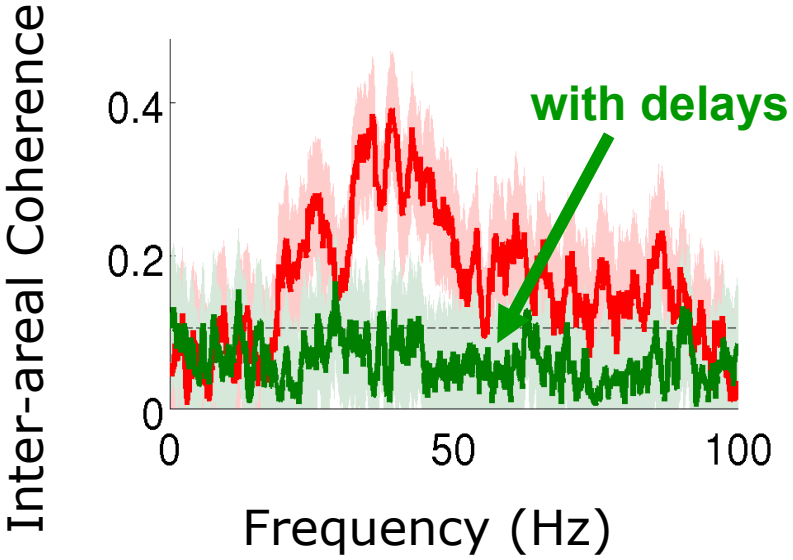


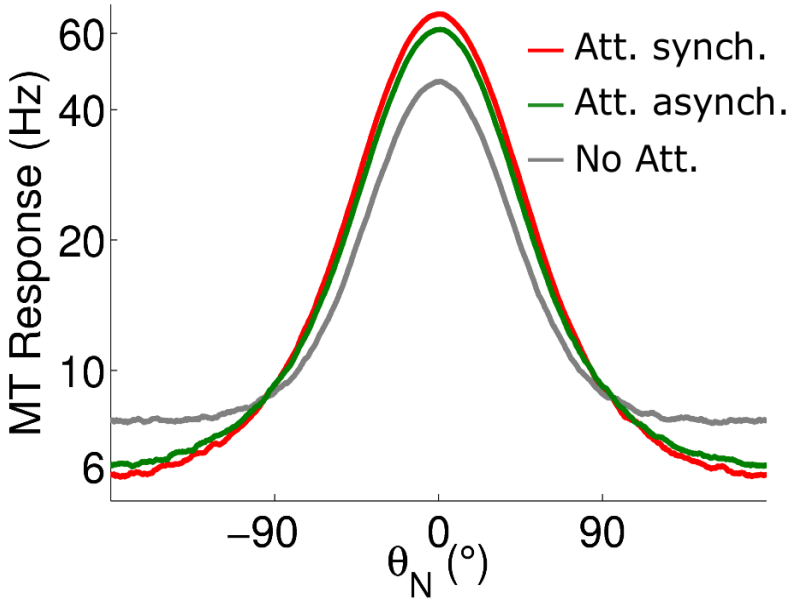


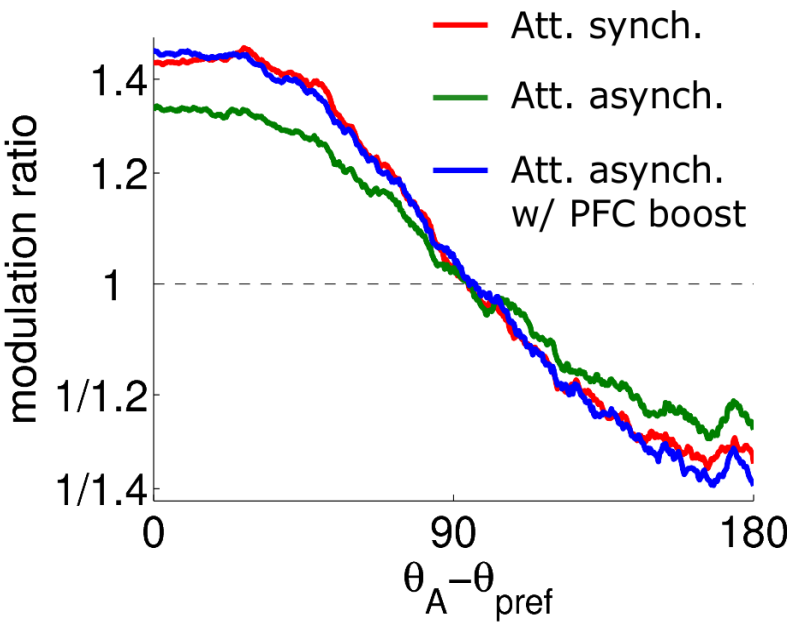
Fries. Trends Cogn Sci 2005

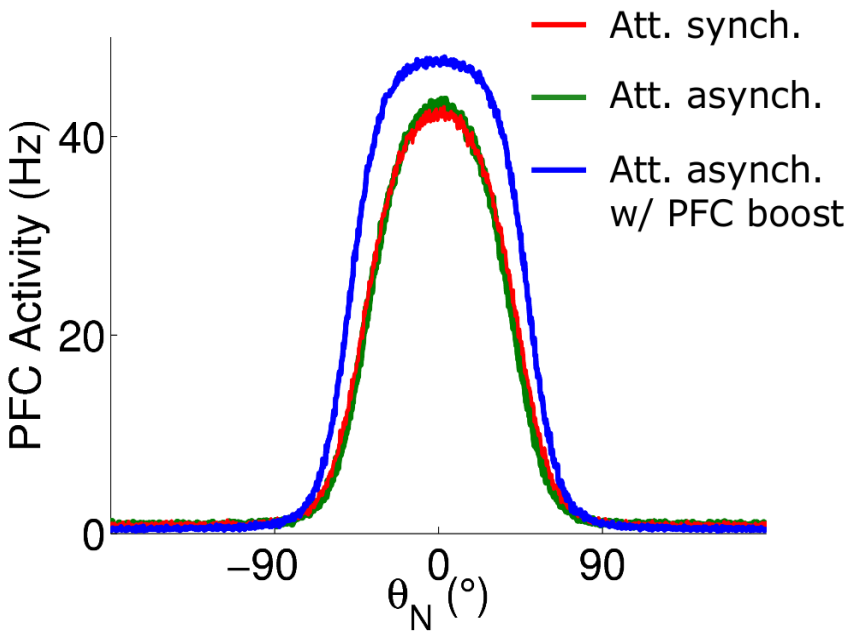

σ
spike in PFC/LIP
dispersion of
random
EPSC latencies
in MT/V4
0
50 ms

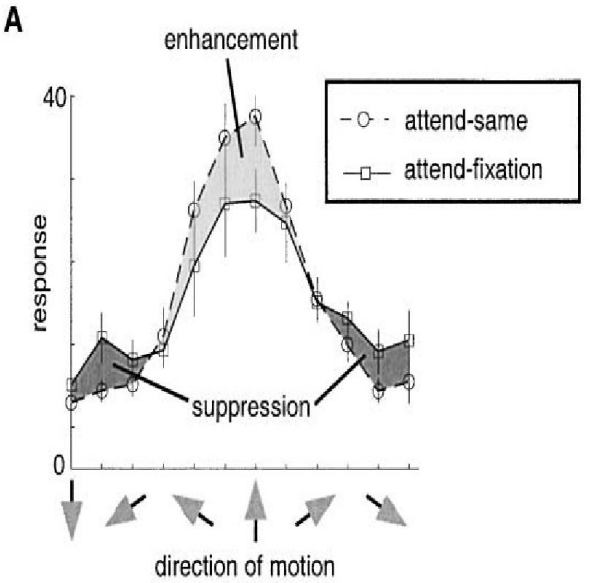

Local Coherence
with delays
0.4
0.2
0
0
50
100
Frequency (Hz)


Inter-areal Coherence
with delays
0.4
0.2
0
0
50
100
Frequency (Hz)


MT Response (Hz)
60
40
20
10
6
Att. synch.
Att. asynch.
No Att.
−90
0
90
θN (°)


modulation ratio
1.4
1.2
1
1/1.2
1/1.4
Att. synch.
Att. asynch.
Att. asynch.
w/ PFC boost
0
90
180
θA−θpref


PFC Activity (Hz)
40
20
0
Att. synch.
Att. asynch.
Att. asynch.
w/ PFC boost
−90
0
90
θN (°)


A
enhancement
40
0
response
attend-same
attend-fixation
suppression
direction of motion

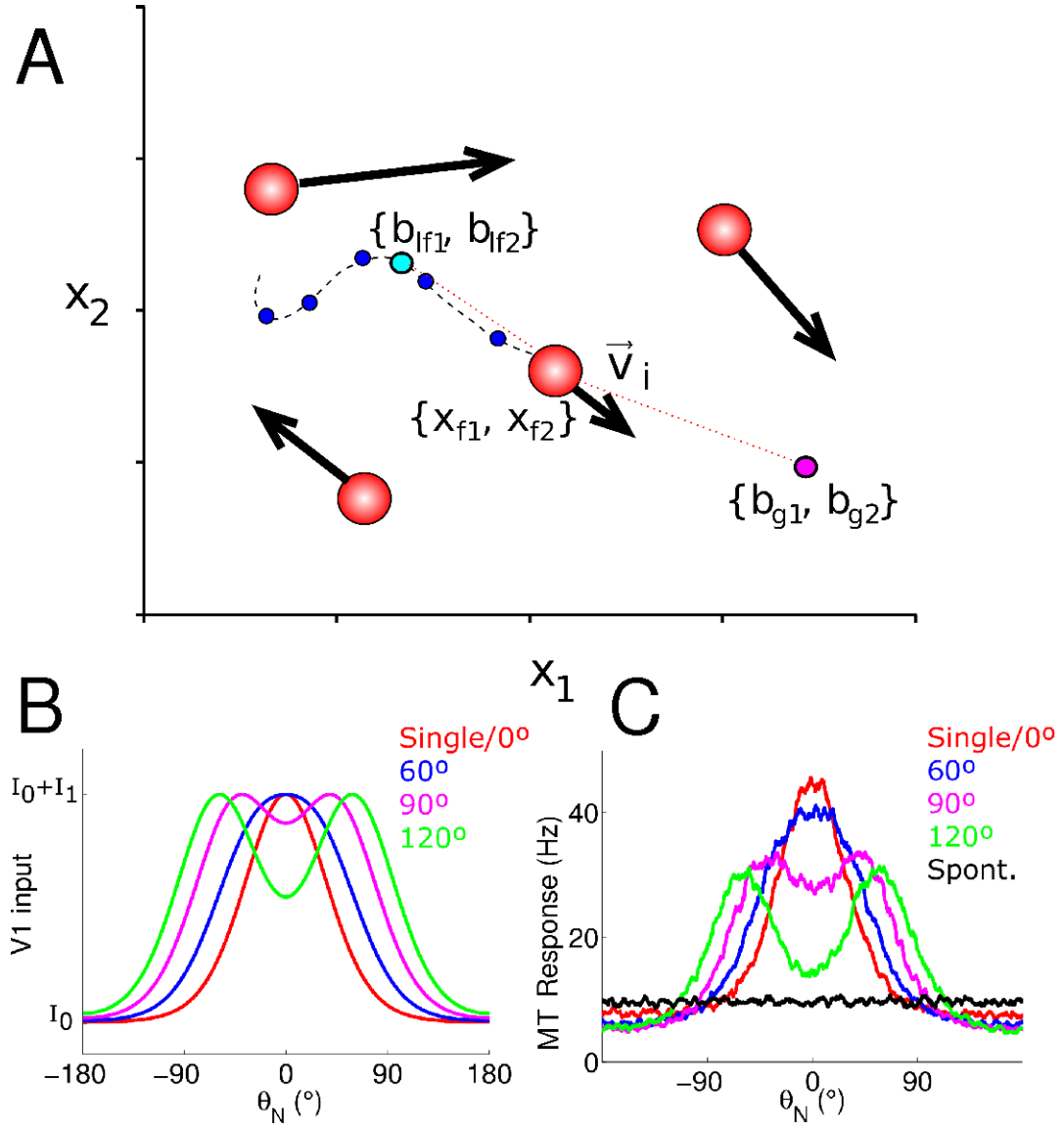
When constrained to show highly irregular spiking activity, oscillatory dynamics failed to show a strong contribution to firing rate modulations in our network model of area MT

How general is this?

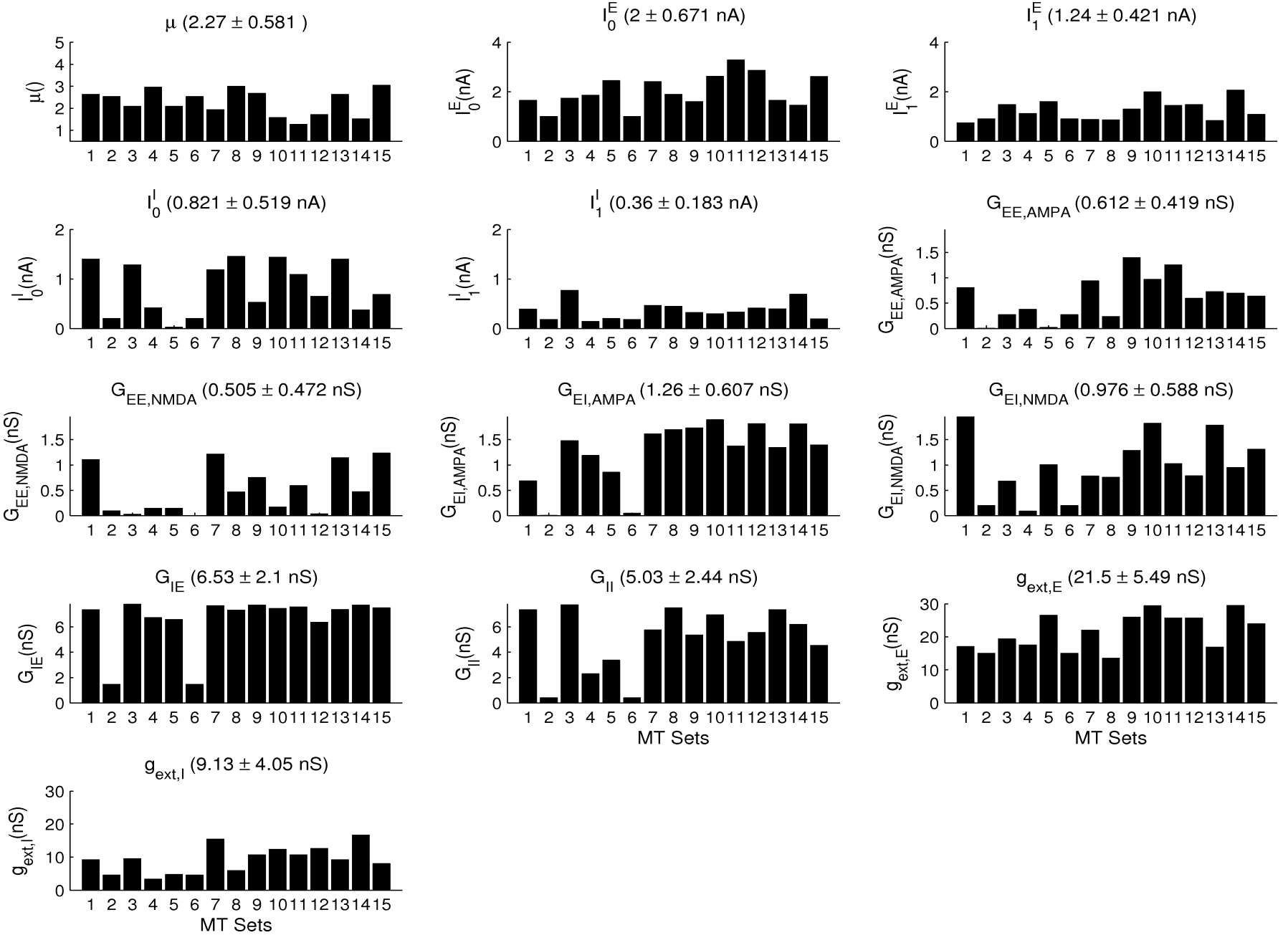
2 methods:

- Brute force
- Mathematical analysis

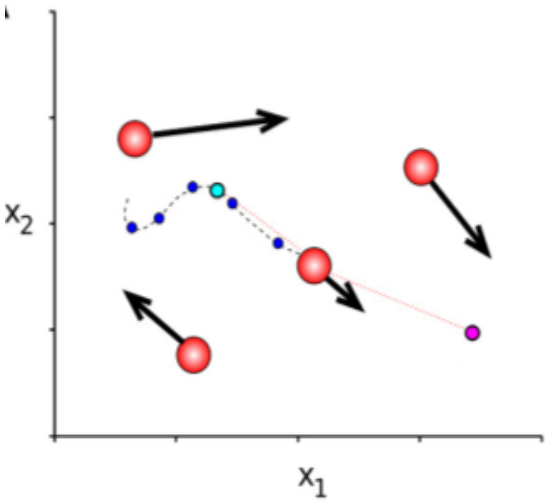
Automated optimization process to find a diversity of MT networks

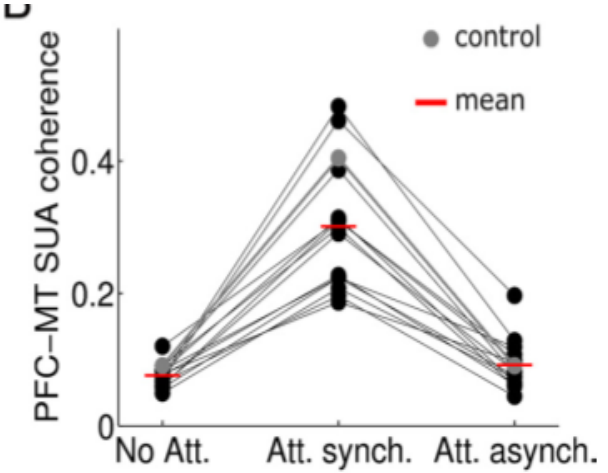


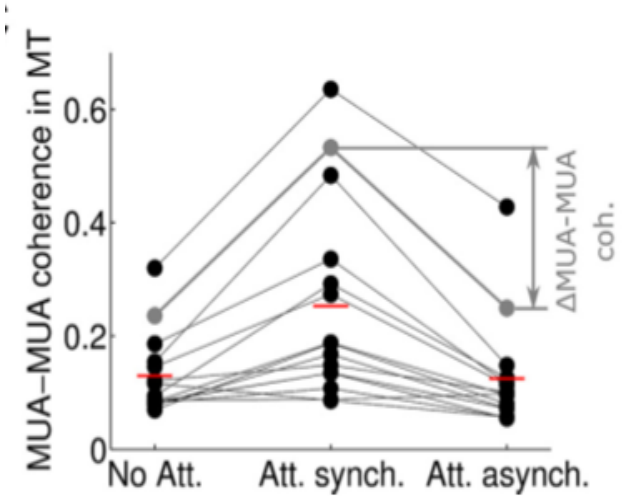
15 MT networks were found with similar functional dynamics but very diverse parameters

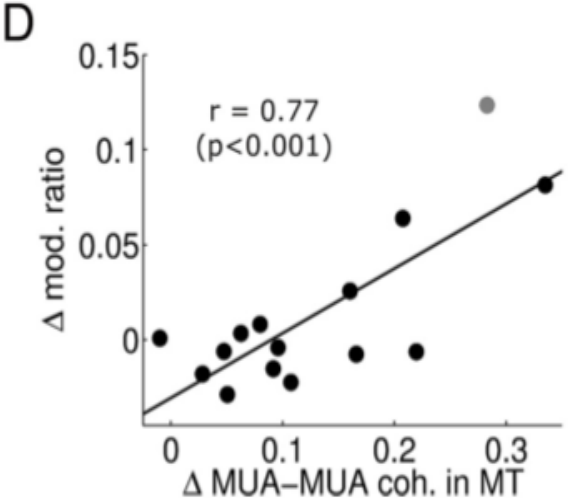


Hook MT to PFC: Introducing random top-down latencies affected little attentional firing rate modulations in ALL 15 networks

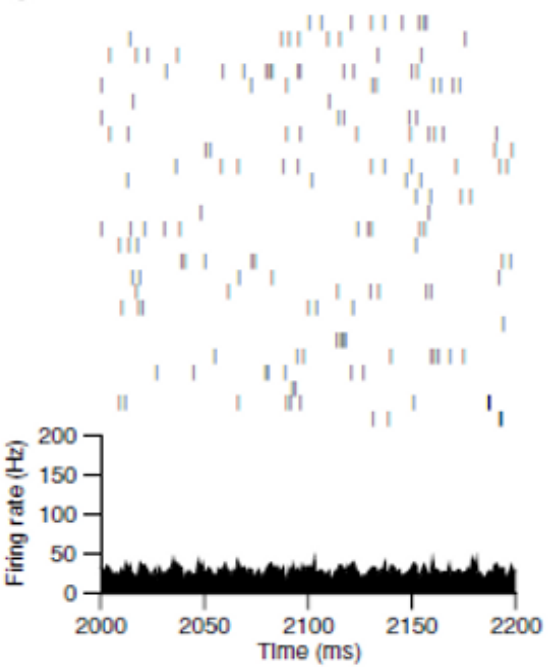


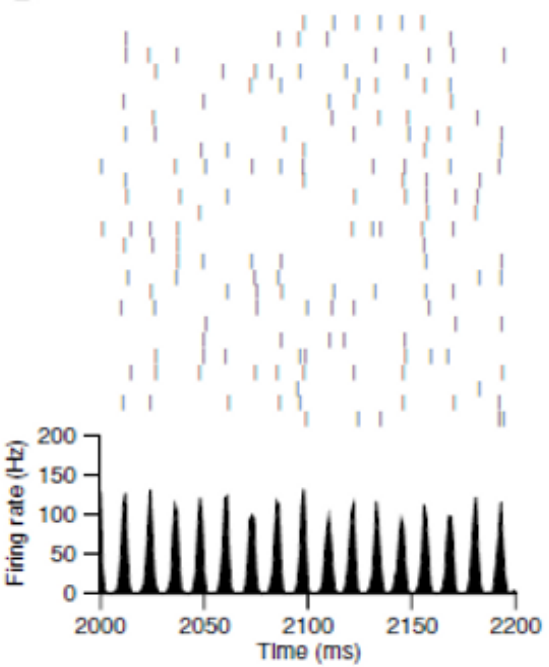


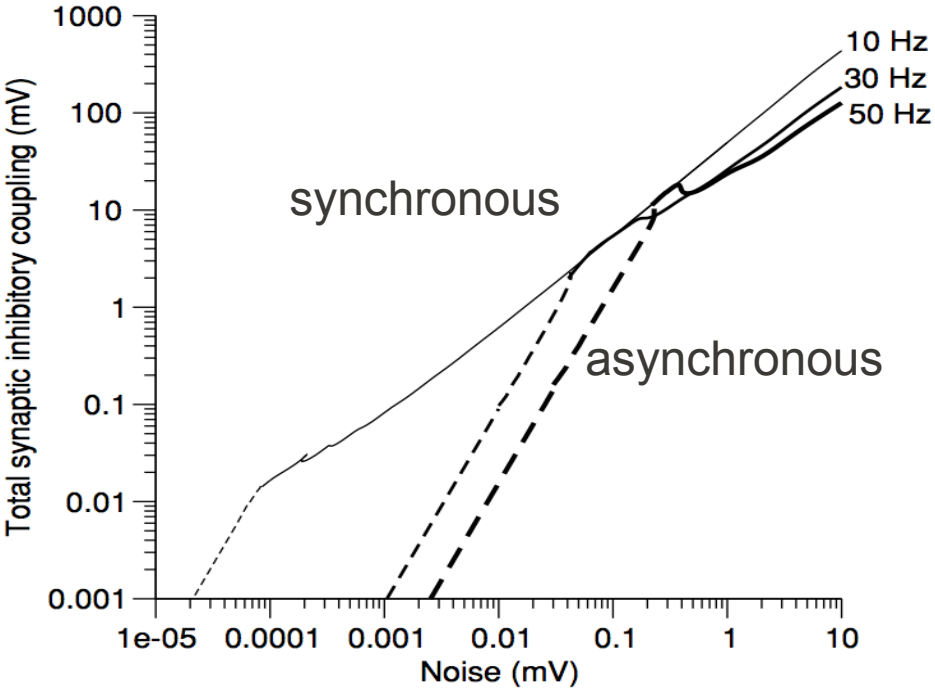




Mathematical approach: simplify to network of inhibitory I&F neurons

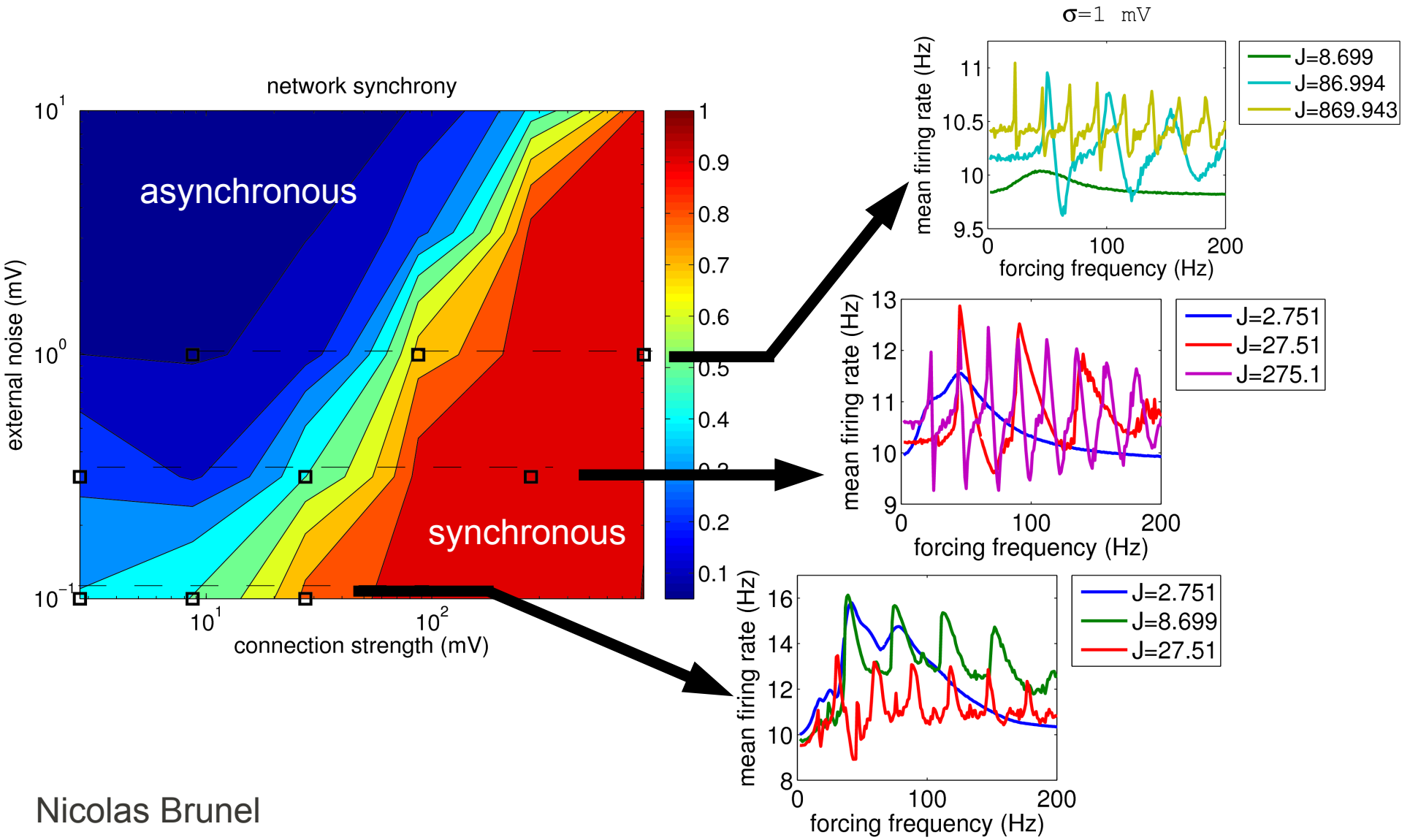






Brunel and Hansel, Neural Comput 2006

Periodic forcing changes mean firing rate especially at bifurcation



Conclusions 2

- Non-modulated highly irregular spiking statistics and strong attentional enhancement of oscillatory network dynamics are compatible in a network model of interacting cortical areas
- When constrained to reconcile spiking statistics and network oscillations, attentional synchrony enhancement does not contribute strongly to firing rate modulations
- However, coherence between areas can be highly selective
- The evaluation of the functional role of oscillations in attention must take into account irregular spiking in the cortex

Thanks to

Salva Ardid (Yale)
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Stefan Treue (Goettingen)
Nicolas Brunel (CNRS,Paris)