Visual Areas Exert Feedforward and Feedback Influences through Distinct Frequency Channels

Bastos et al., 2015

Orhan Soyuhos

What is Granger Causality?

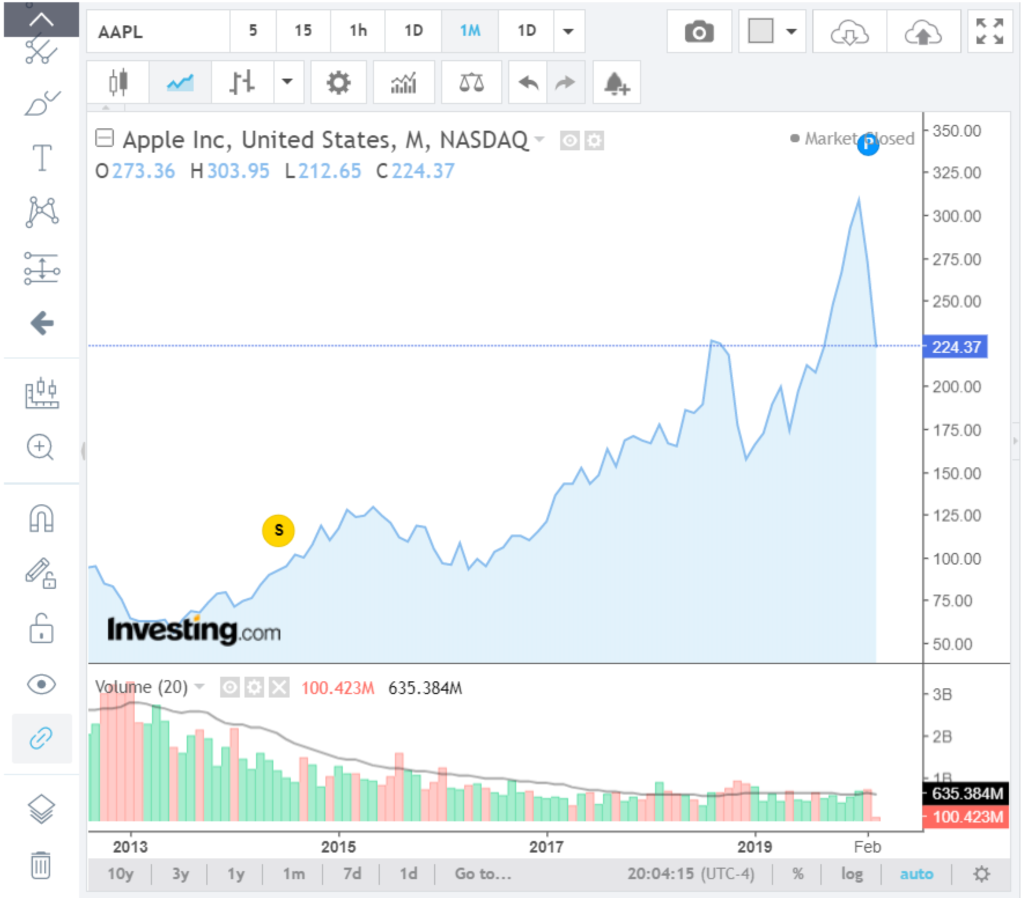
Optional material

Granger Causality

- Clive Granger
  - econometrician
  - Nobel Prize winner
  - non-linear time series

- "based on the simple idea that causes both precede and help predict their effects." (Anil et al., 2015)

https://en.wikipedia.org/wiki/Clive_Granger



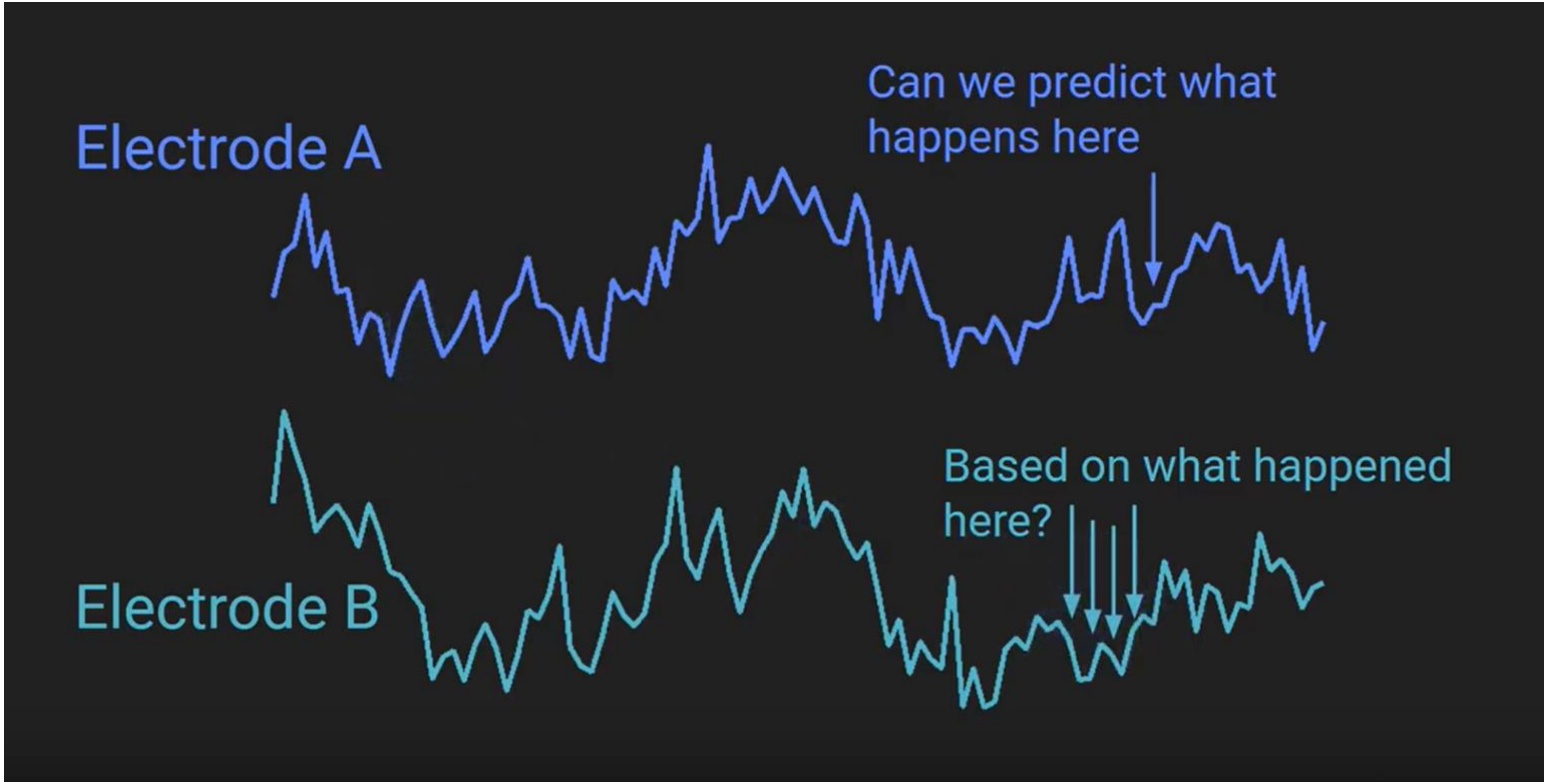
Symbol	Last	Chng (%)
AAPL •	224.37	-4.87 (-2.12%)
BABA •	176.34	-4.96 (-2.74%)
TWTR •	24.69	+0.74 (+3.09%)
IBM •	94.77	-0.62 (-0.65%)
BAC •	18.08	-1.59 (-8.08%)
KO •	37.56	-0.74 (-1.93%)
XOM •	31.45	-1.29 (-3.94%)
FB •	148.10	-1.63 (-1.09%)
F •	4.01	-0.32 (-7.39%)
GM •	17.60	-0.54 (-2.98%)
GOOGL •	1054.13	-14.08 (-1.32%)
HPQ •	13.70	-0.25 (-1.79%)
AA •	5.67	+0.19 (+3.47%)
JPM •	79.03	-4.47 (-5.35%)
MCD •	137.10	-11.39 (-7.67%)
MSFT •	135.98	-1.37 (-1.00%)
SBUX •	56.55	-1.48 (-2.55%)

https://www.investing.com/charts/stocks-charts

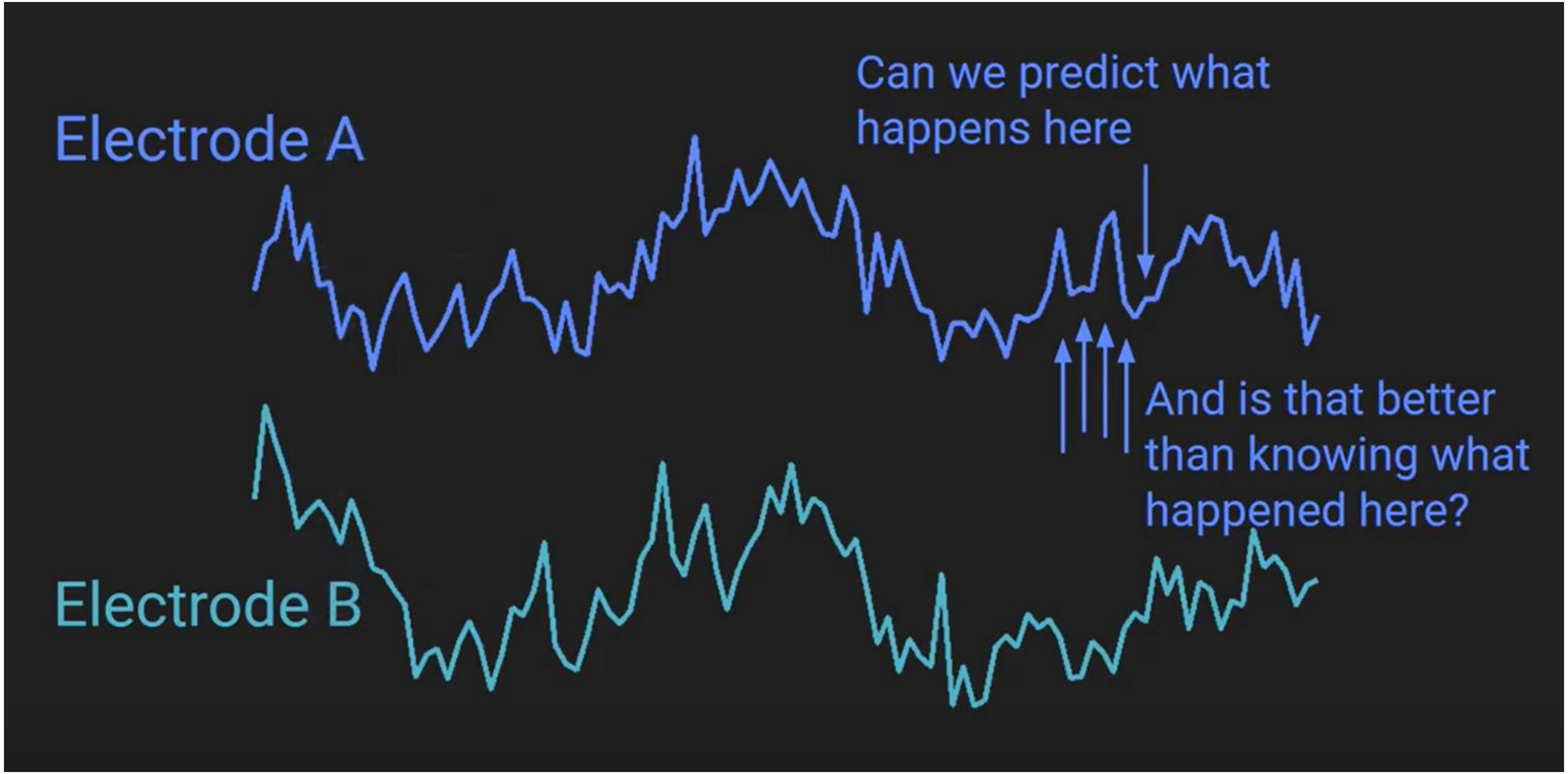
Granger "Prediction"

- Cohen, 2014
- Granger causality does not imply nor require causality.
- "G-causality says that a variable X "G-causes" another variable Y if the past of X contains information that helps predict the future of Y, over and above the information already in the past of Y itself (and in the past of other "conditioning" variables Z)." (Anil et al., 2015)
- G-causality vs:
  - correlation or coherence

Application in Neuroscience



Mike X Cohen, https://www.youtube.com/watch?v=XqsSB_vpHLs



Mike X Cohen, https://www.youtube.com/watch?v=XqsSB_vpHLs

Autoregressive models

- Univariate autoregressive models

$$\mathbf{X}_t = a_1\mathbf{X}_{t-1} + a_2\mathbf{X}_{t-2} + \ldots + a_n\mathbf{X}_{t-n} \quad + e_{tx}$$
$$\mathbf{Y}_t = b_1\mathbf{Y}_{t-1} + b_2\mathbf{Y}_{t-2} + \ldots + b_n\mathbf{Y}_{t-n} \quad + e_{ty}$$

- Bivariate autoregressive models

$$\mathbf{X}_t = a_1\mathbf{X}_{t-1} + \ldots + b_1\mathbf{Y}_{t-1} + \ldots + \epsilon_{txy}$$

Mike X Cohen, https://www.youtube.com/watch?v=XqsSB_vpHLs

Autoregressive models

- Univariate autoregressive models

$$\mathbf{X}_t = \sum_{n=1}^{k} a_n \mathbf{X}_{t-n} + e_t$$

- Bivariate autoregressive models

$$\mathbf{X}_t = \sum_{n=1}^{k} a_n \mathbf{X}_{t-n} + \sum_{n=1}^{k} b_n \mathbf{y}_{t-n} + \epsilon_t$$

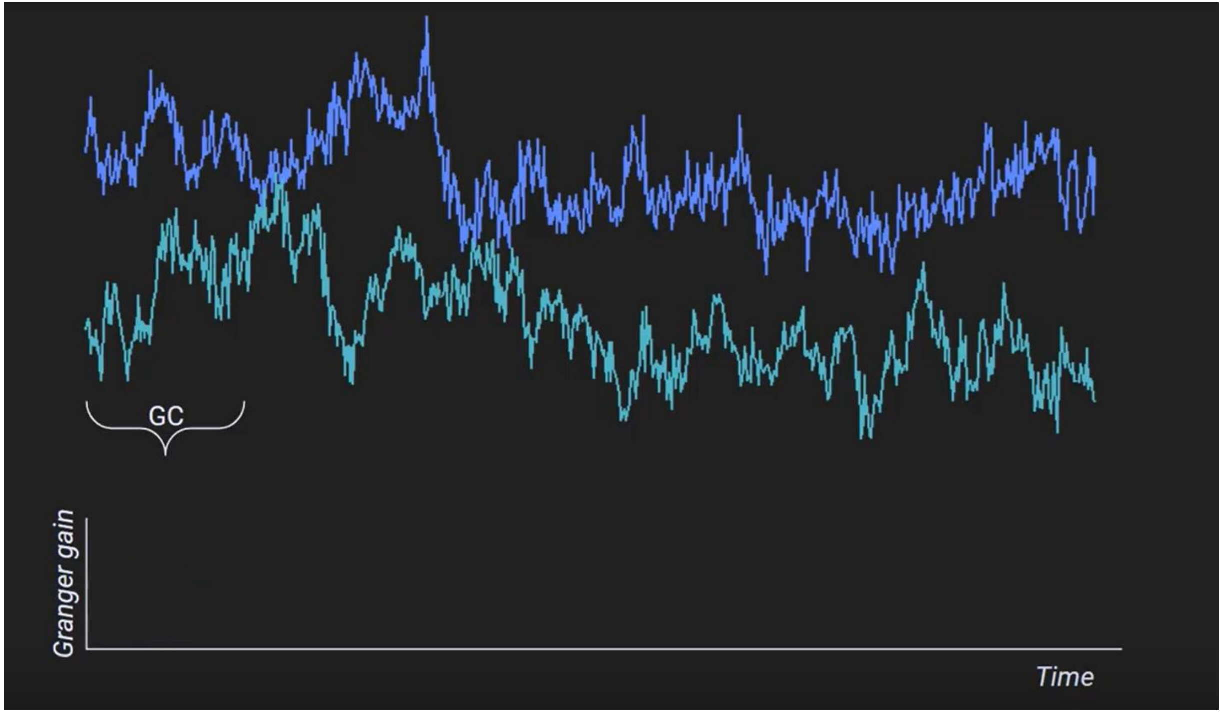
Mike X Cohen, https://www.youtube.com/watch?v=XqsSB_vpHLs

Prediction errors

$$GC = \log\left(\frac{\mathrm{Var}[e]}{\mathrm{Var}[\epsilon]}\right)$$

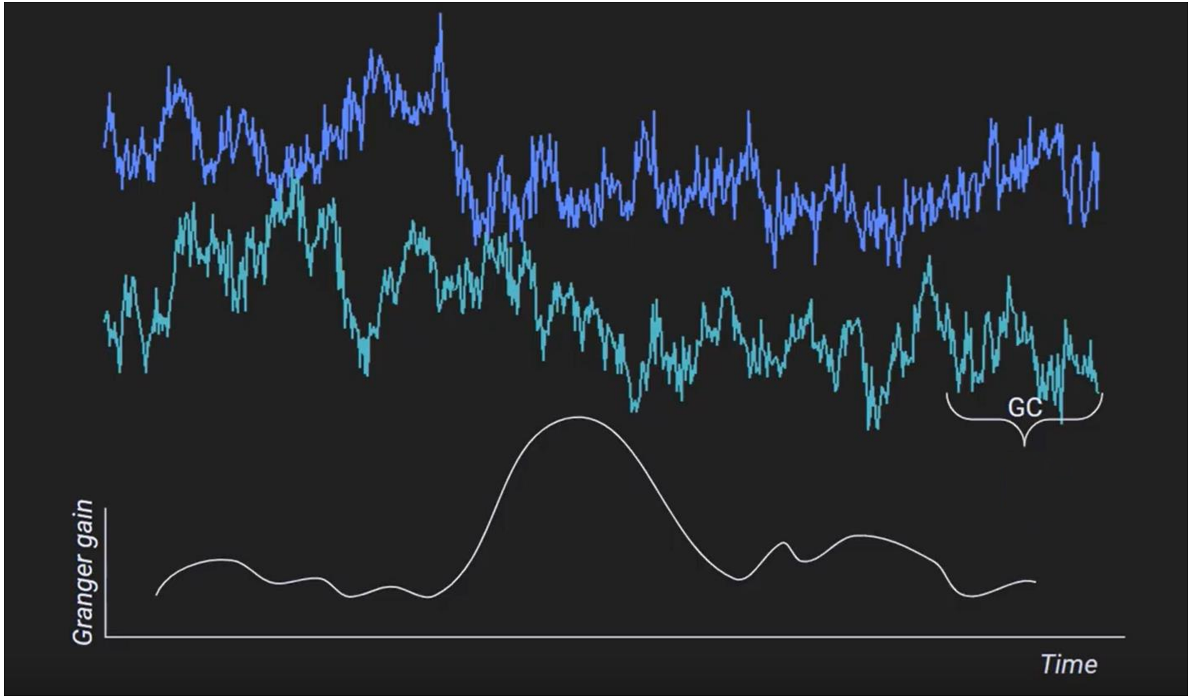
Mike X Cohen, https://www.youtube.com/watch?v=XqsSB_vpHLs

Granger Parameters: time window



Mike X Cohen, https://www.youtube.com/watch?v=XqsSB_vpHLs

Granger Parameters: time window



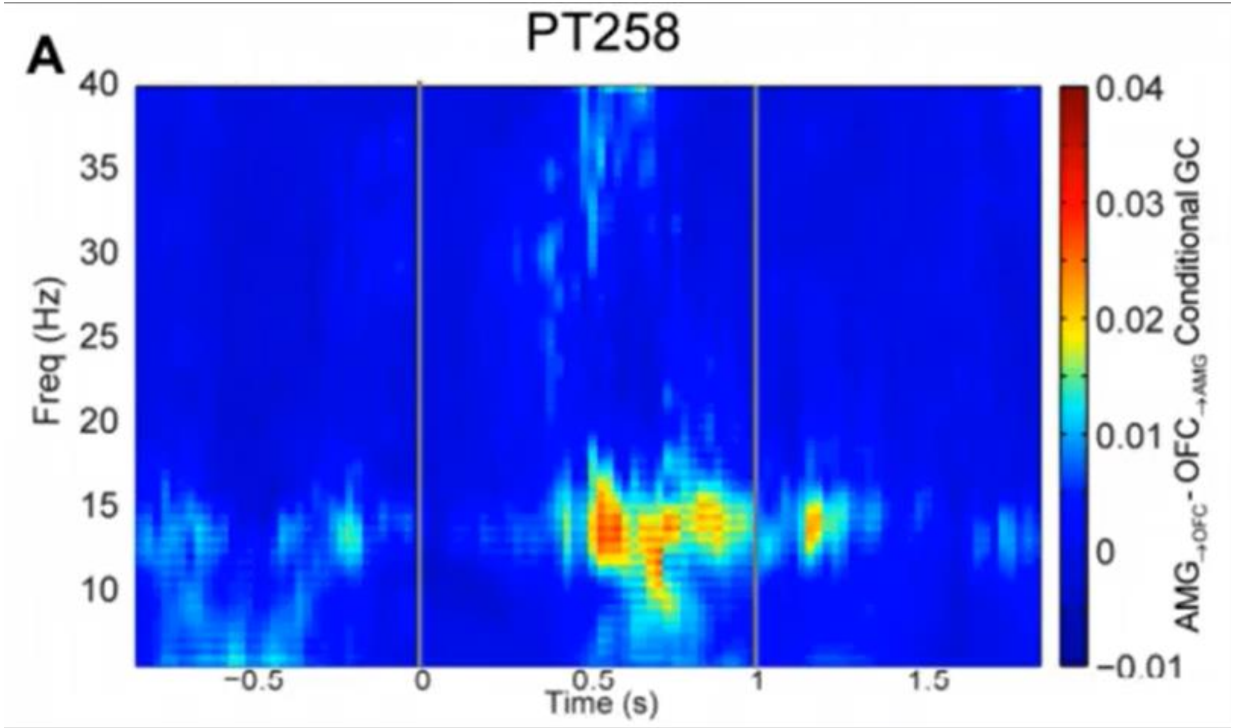
Mike X Cohen, https://www.youtube.com/watch?v=XqsSB_vpHLs

Granger Parameters: model order

$$\mathbf{X}_t = \sum_{n=1}^{k} a_n \mathbf{X}_{t-n} + \sum_{n=1}^{k} b_n \mathbf{y}_{t-n} + \epsilon_t$$

Mike X Cohen, https://www.youtube.com/watch?v=XqsSB_vpHLs

Spectral Granger Causality



Jenison, 2014, PLoS One

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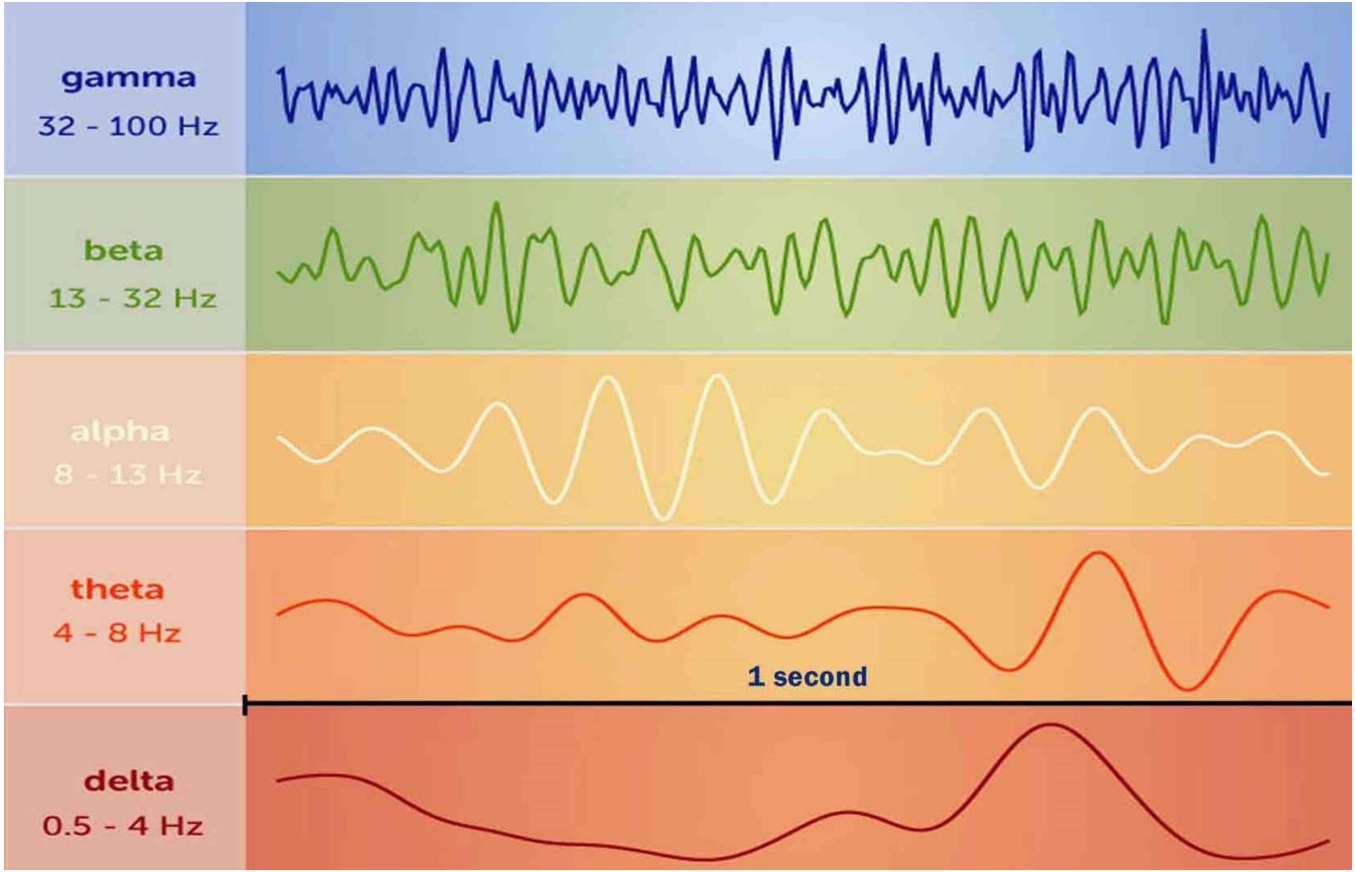
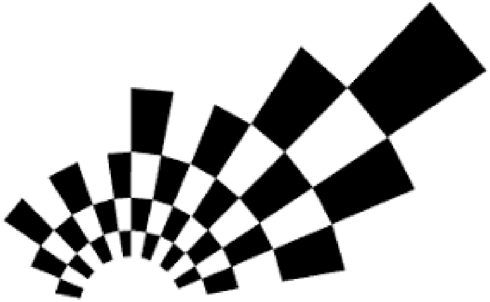


https://psychedelicreview.com/altered-oscillations-the-modulatory-effect-of-dmt-on-brain-waves/

Introduction: What we know?

- “Many aspects of cognitive performance can only be explained through the concept of feedback influences.”

- Behavioral studies
- Neurophysiological studies



- “Recent studies have documented a **neurophysiological asymmetry** between the layers of visual cortex.”

Neurophysiological asymmetry

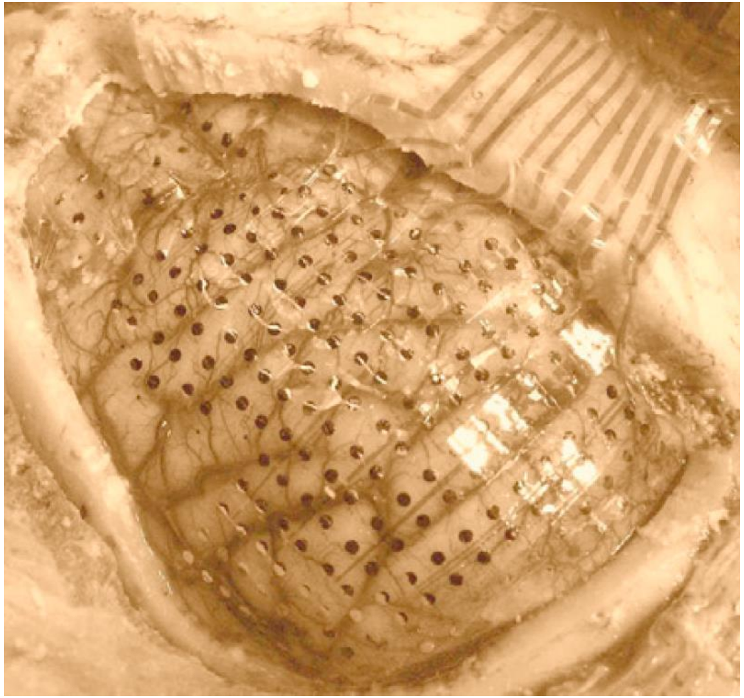
- **supragranular layers** → local gamma-band synchronization
- **infragranular layers** → local alpha/beta-band synchronization

- Local rhythmic synchronization can lead to **interareal synchronization**
  - possible mechanism of effective interareal interaction

- **Hypothesis:**
  - “interareal synchronization in the **gamma-frequency** band might mediate **feedforward** influences, and interareal synchronization in the **beta-frequency** band might mediate **feedback** influence”

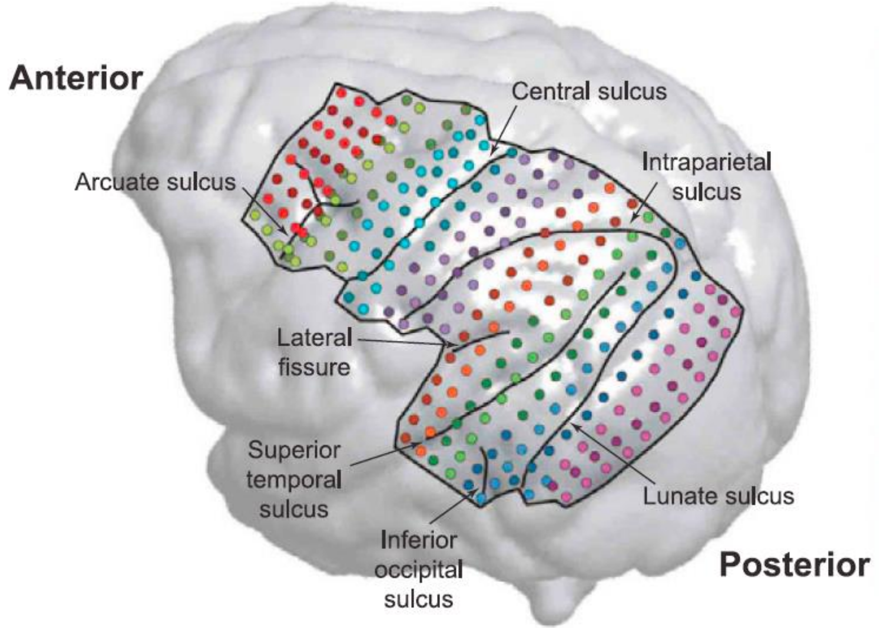
Experimental Procedure

- electrocorticography (ECoG) grids
  - left hemispheres of two macaque monkeys
  - local field potentials (LFPs)
- visuospatial attention task

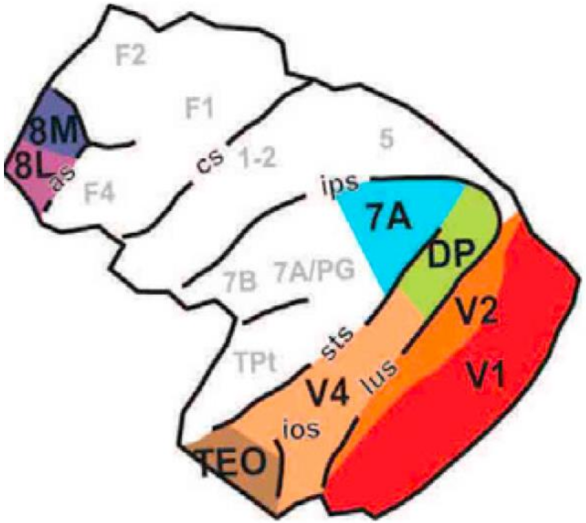


The brain of monkey 1 after placement of the ECoG grid.

Electrocorticography (ECoG) grids

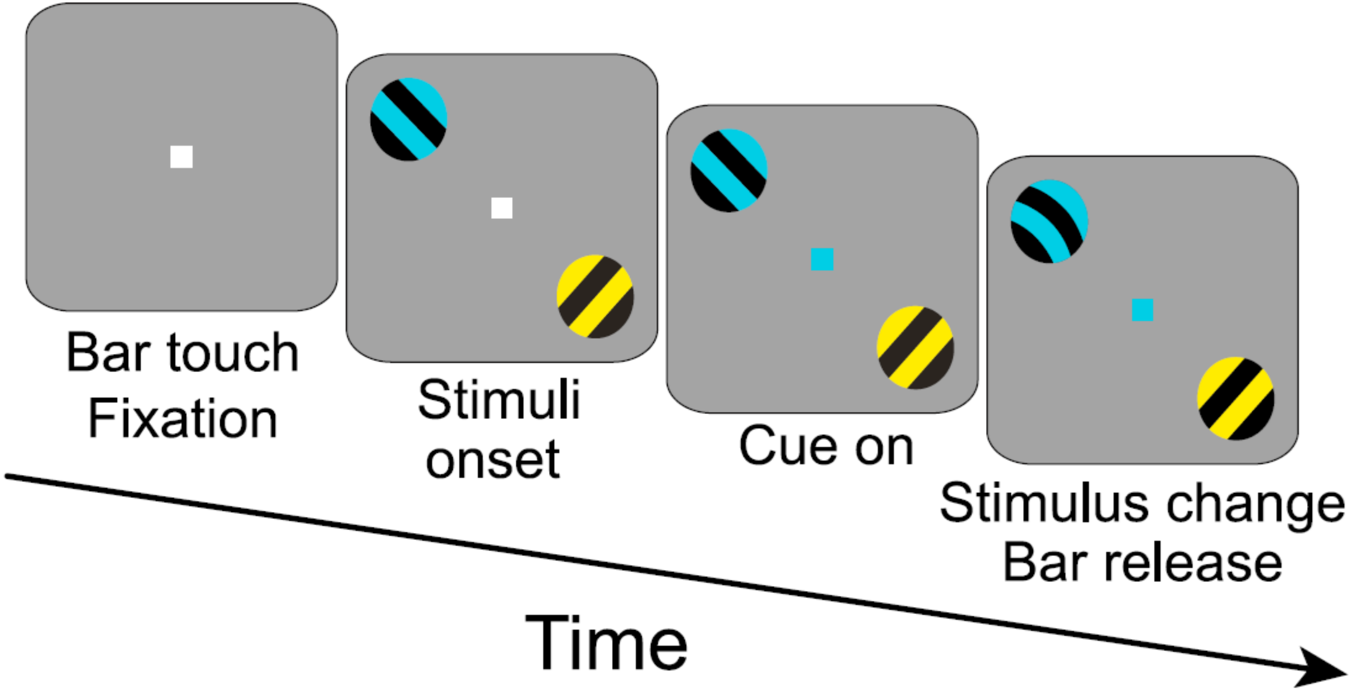


Rendering of the brain of monkey 1 based on structural MRI scans.

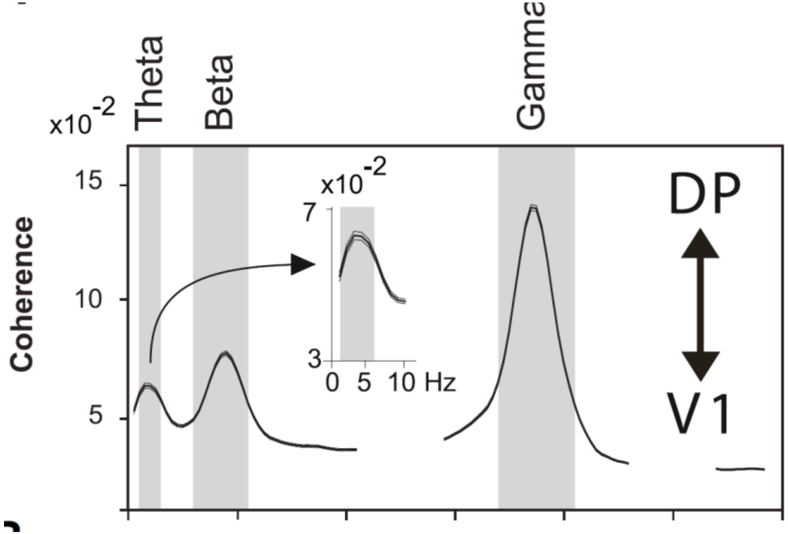


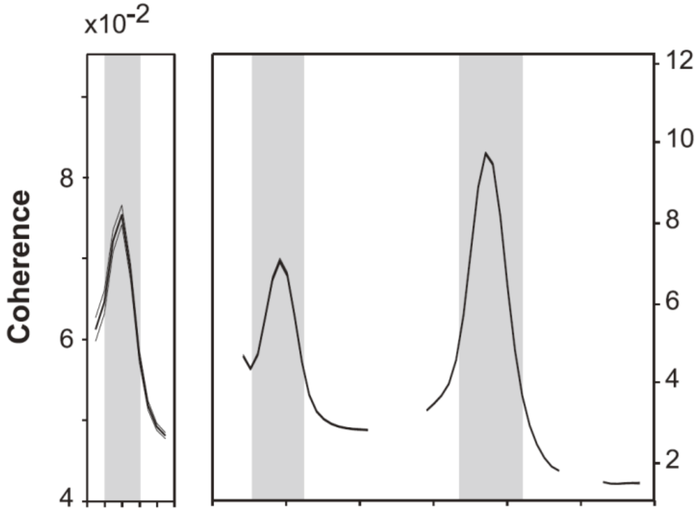
Parcellation of ECoG-covered regions into cortical areas.

Selective visual attention task



1) Interareal Synchronization Occurs in Narrow Theta, Beta, and Gamma Frequency Bands





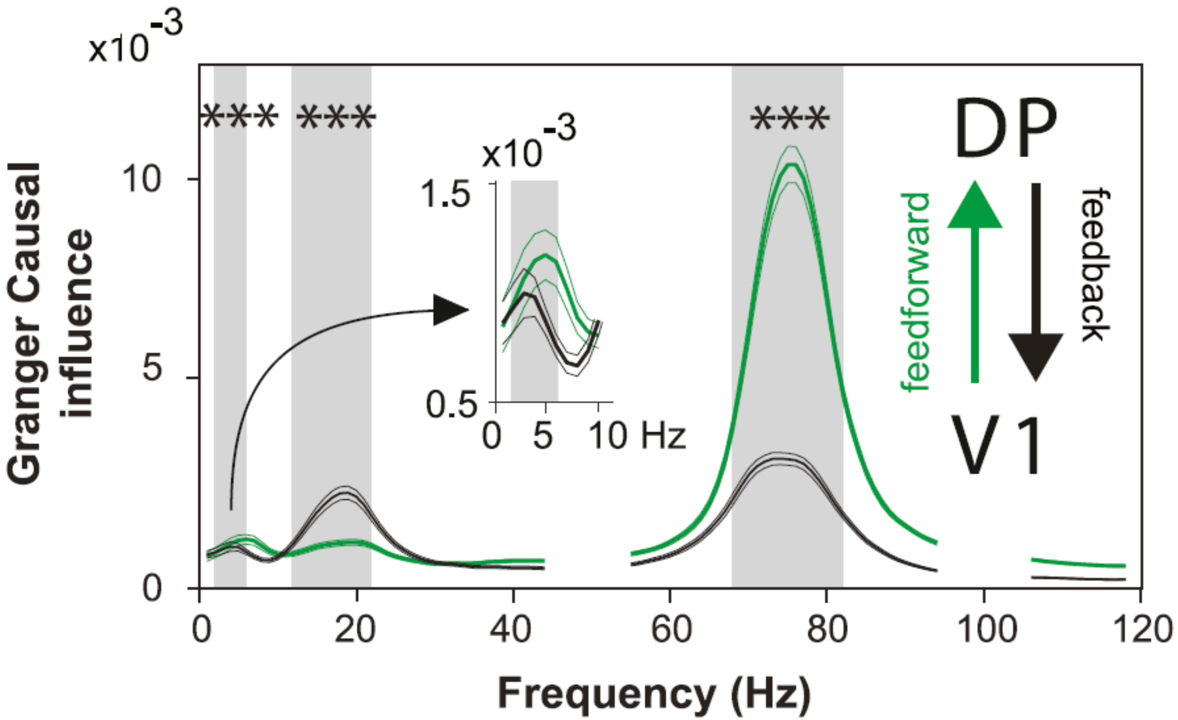
- Coherence spectra for an example pair of areas: V1 and DP, from monkey 1.
- All interareal coherence spectra were averaged, and peaks were found using an automatic peak-detecting algorithm

- Between pairs of sites from different areas, interareal synchronization is quantified by the **coherence metric**.

- Frequency-specific directed influences are determined by calculating **Granger-causal (GC) influences** between all possible interareal pairs of sites

- “The spectrum of GC influences of site 1 onto site 2 quantifies, per frequency, the variance in site 2 that is not explained by the past of site 2, but by the past of site 1.”

Granger-causal (GC) influences



The GC feedforward influence was stronger than the feedback influence in the theta and gamma-bands, whereas the feedback influence was stronger in the beta-band

2) Asymmetries in Granger-Causal Influences Relate to Anatomical Asymmetries

- In the paper, GC influences are related to anatomical projections, specifically to a metric of their feedforward or feedback character.

- What we know already: (Felleman and Van Essen, 1991)
    - **Feedforward** connections originate preferentially in **supragranular layers**.
    - **Feedback** connections originate preferentially in the **infragranular layers**.

- Which tools we have:
    - **Neuronal tracing**

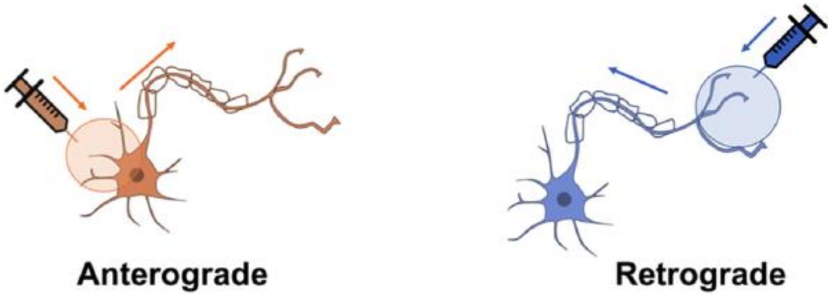
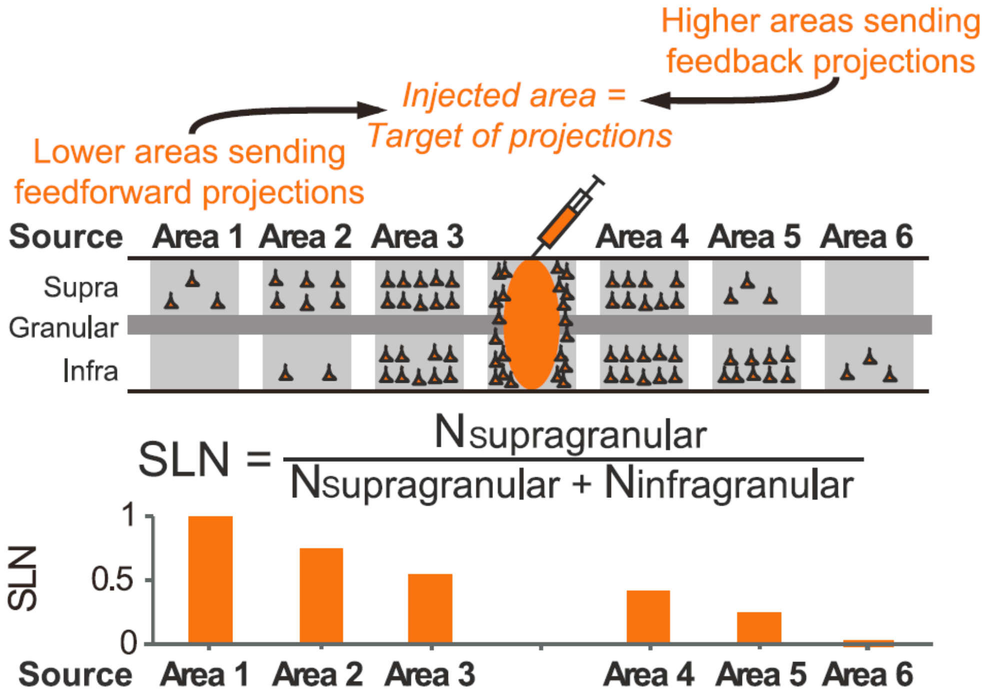


Figure 2: Directions of neuronal tracing: The tracer spreads as shown by the arrows, either away from the cell body (anterograde) or towards it (retrograde). https://blog.addgene.org/using-aav-for-neuronal-tracing



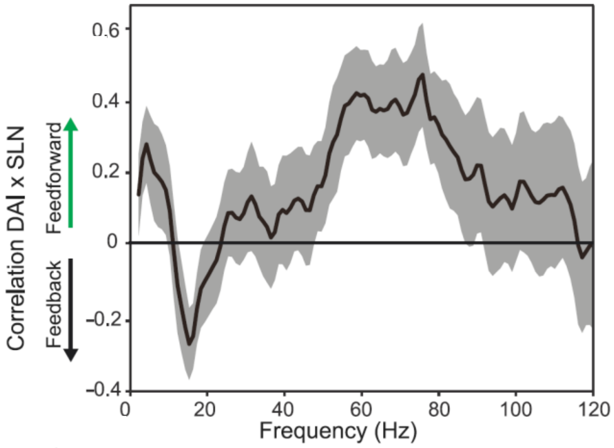
Retrograde tracer is injected into a target area and labels neurons in several source areas projecting to the target area

SLN are related to the corresponding GC influence (GCIs)

- DAI:
  - The directed influence asymmetry index:

$$[GCI(source\text{-}>target) - GCI(target\text{-}>source)] / [GCI(source\text{-}>target) + GCI(target\text{-}>source)]$$

- DAI values are correlated with the corresponding SLN values, across all area pairs.



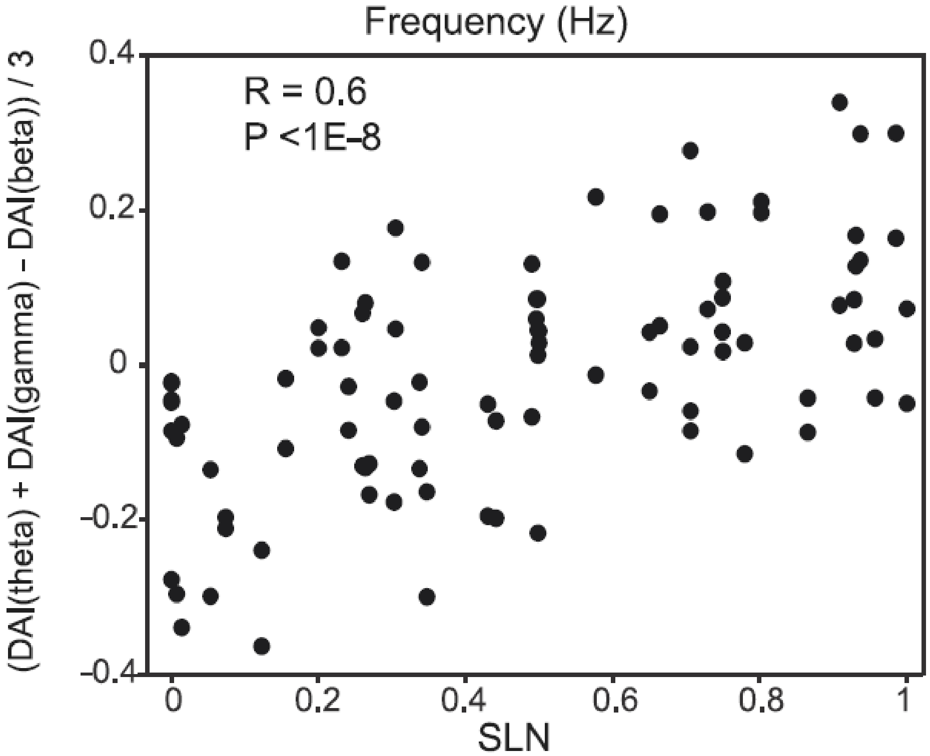
*Spearman rank correlation between DAI values and SLN values

3) Asymmetries in Granger-Causal Influences Define a Functional Hierarchy

- “The correlations between the anatomical SLN metric and the functional DAI metric suggest that it might be possible to construct a hierarchy of visual cortical areas **from DAI values alone**.”

- **Firstly:**
    - the post-cue period was used
    - combined all evidence available in the DAIs across the frequency spectrum
        - by averaging the DAIs of the theta-, beta-, and gamma-frequency bands

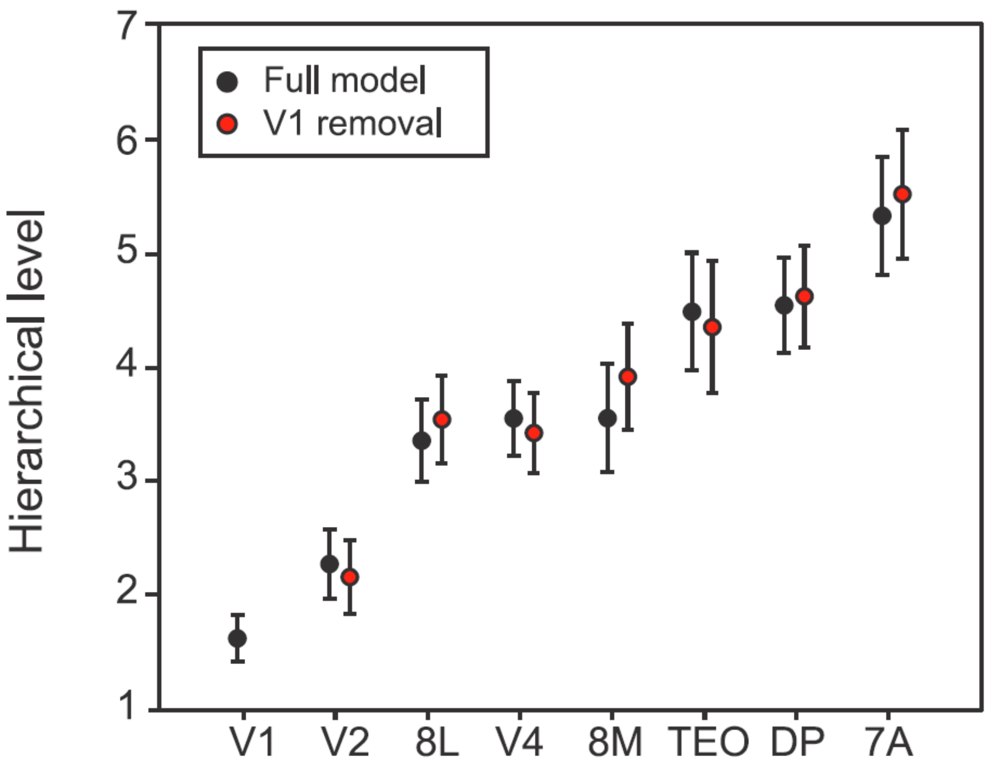
    - This **multifrequency band DAI (mDAI)** was strongly correlated with the SLN across all pairs of areas



Correlation between SLN and the DAI combined across theta-, beta-, and gamma-bands as specified on the y axis.

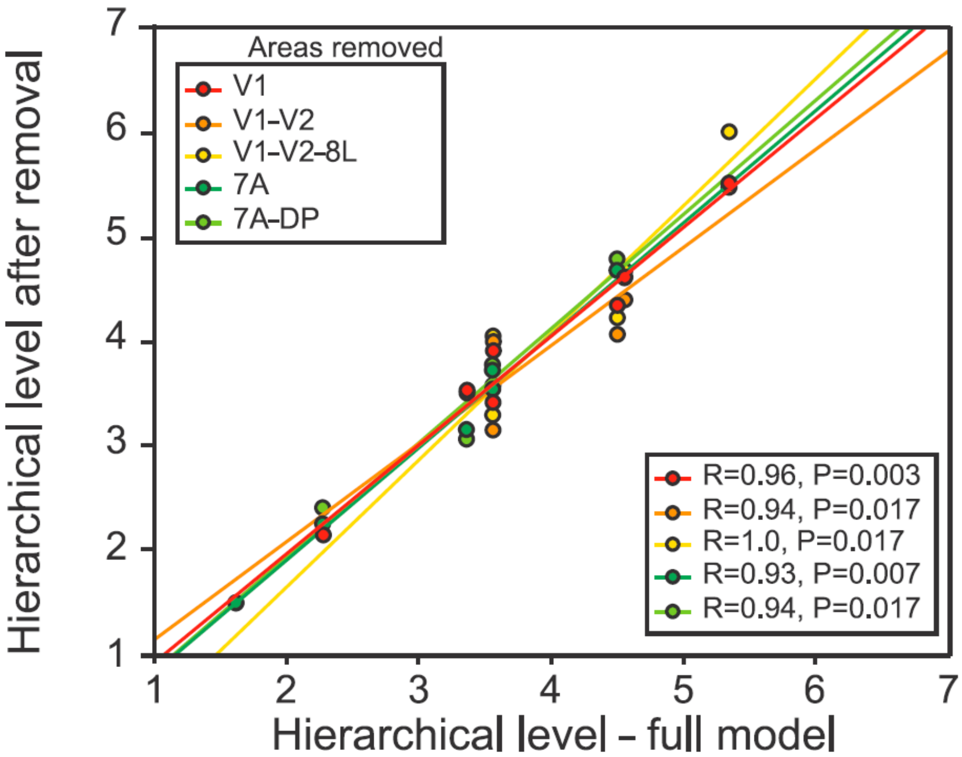
**Spearman rank correlation is used*

- **Secondly:**
  - The mDAI values, which can range from -1 to 1, were **rescaled** into a range from -5 to 5.
  - **Each area** is considered as target area
  - The rescaled mDAI values of all source areas are **shifted** such that the smallest value was one (1 to 10).
  - The resulting functional-hierarchical levels are **averaged** across all target areas and across the two monkeys.



The existence of a GC-influence-based functional hierarchy.

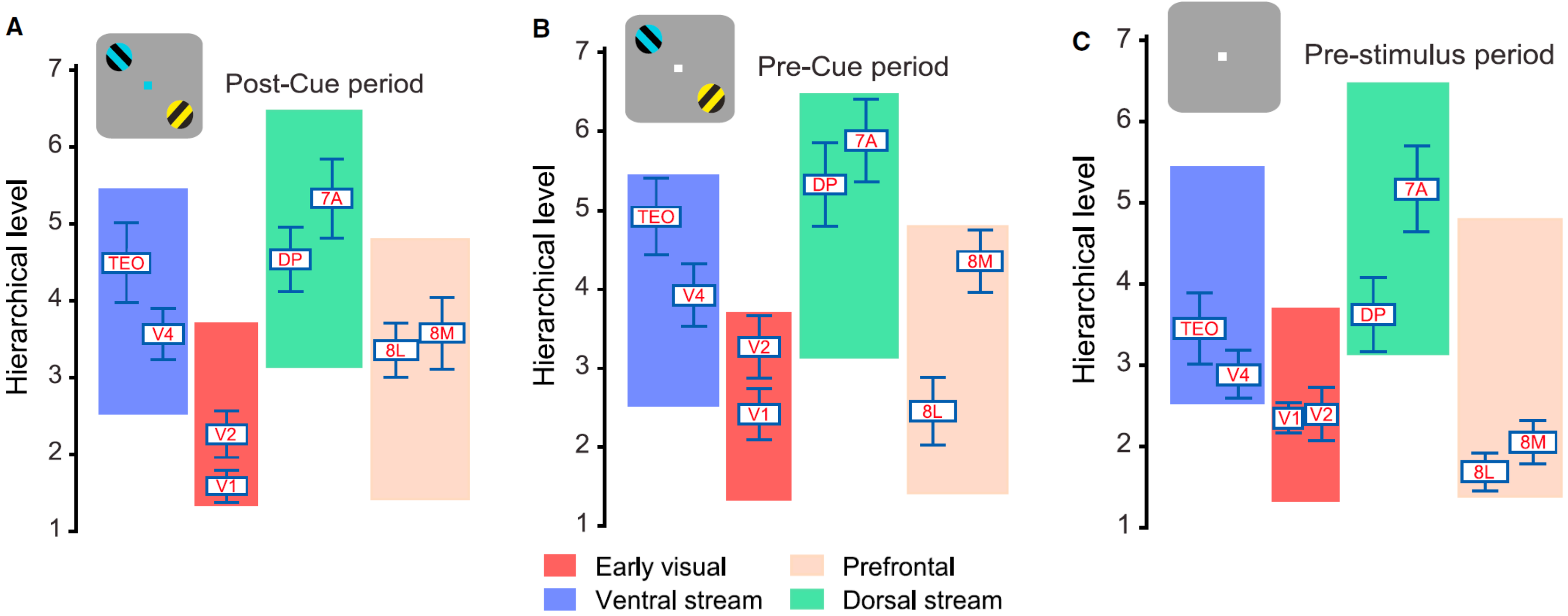
*This functional hierarchy correlates strongly with the most recent anatomical hierarchy (Markov et al., 2014b) of visual cortex ($R = 0.93$, $p = 0.002$).



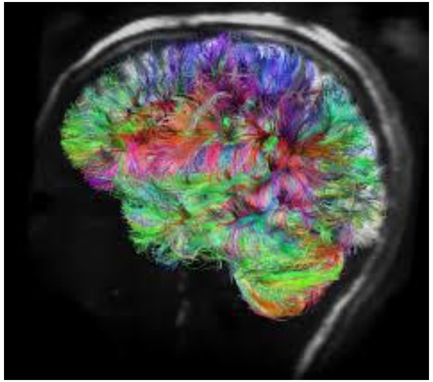
“Revealing immunity to manipulations”

4) Functional Hierarchy Changes Dynamically with Behavioral Context

- The functional hierarchy changes **across different task periods**.

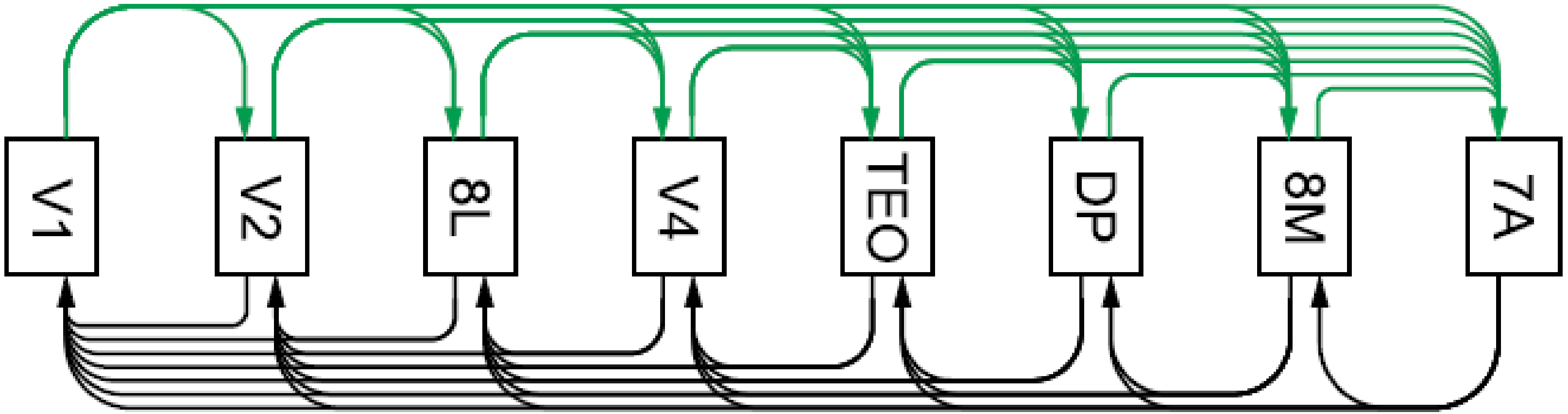


- **The Functional Hierarchy Is Dynamic:**
  - It is not fixed as are anatomy- based hierarchies.
  - The most recent anatomy-based hierarchy (Markov et al., 2014b) shows:
    - an **R = 0.93** correlation to the **post-cue** functional hierarchy
    - an **R = 0.91** correlation to the **pre-cue** functional hierarchy
    - and **no** significant correlation to the **pre-stimulus** functional hierarchy
  - Though anatomical connections in the two directions are present at all times.



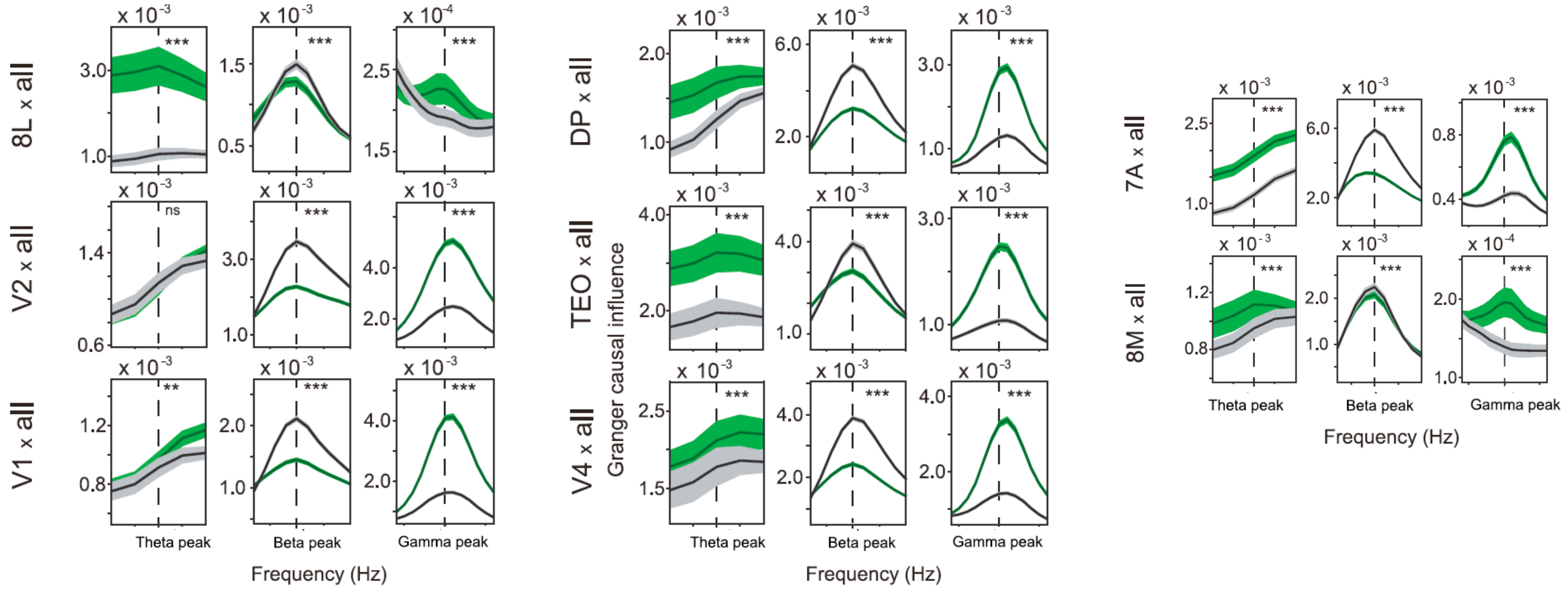
5) Global Consistency of the Functional and Anatomical Hierarchies

- Hierarchical ranking of the recorded visual areas according to the most recent **anatomical hierarchical model** (Markov et al., 2014b).



This hierarchical model specifies each interareal influence as either bottom-up or top-down.

- Each target area’s GC influences to all other areas were **sorted into bottom up and top-down influences.**



Spectra were averaged across monkeys after aligning frequency peaks.

6) Attention Enhances Top-Down and Bottom-up Influences in a Spatially Specific Manner

- Top-down control is expected to be enhanced by selective attention.

- Bressler and Richter, 2014; Lee et al., 2013:
    - When selective attention was directed to the contralateral as compared to the ipsilateral stimulus, **top-down beta-band** GC influences were enhanced.

- This enhanced top-down beta-band influence might lead to enhanced bottom-up gamma-band influence:
    - when selective attention was directed to the contralateral as compared to the ipsilateral stimulus, **bottom-up gamma-band** GC influences were enhanced in the grand average

Results

1. Interareal Synchronization Occurs in Narrow Theta, Beta, and Gamma Frequency Bands
2. Asymmetries in Granger-Causal Influences Relate to Anatomical Asymmetries
3. Asymmetries in Granger-Causal Influences Define a Functional Hierarchy
4. Functional Hierarchy Changes Dynamically with Behavioral Context
5. Global Consistency of the Functional and Anatomical Hierarchies
6. Attention Enhances Top-Down and Bottom-up Influences in a Spatially Specific Manner

Discussion

- Asymmetries in directed influences are likely related to the **laminar pattern** of interareal anatomical projections.

- Feedforward and feedback interareal influences need to fulfill **different requirements**, which might be met by synchronization in different frequency bands.

- Inputs may have differential effects at their target structure uniquely due to the rhythm through which they have been transferred:
  - **functional tagging**

Discussion

- Functional hierarchy exhibits dynamic changes. This might be due to differential activation of superficial and deep layers.
  - **predictive coding** (Bastos et al., 2012):
    - The statistical regularities of sensory inputs are learned by **shaping feedforward connectivity**
  - evidences from previous studies:
    - von Stein et al., 2000
    - Arnal et al., 2011
    - In these studies, the response to the predicted stimulus entailed a lower and the response to the unpredicted stimulus a higher frequency band.

- The operationalization of feedforward versus feedback signaling through cognitive tasks remains a **challenge**:
  - Enhanced bottom-up signaling can be a consequence of enhanced top-down signaling

Discussion

- The definition of the functional hierarchy through the assessment of interareal GC influences might be **transferable to human experiments**.
    - “Intracranial LFP recordings (Tallon-Baudry et al., 2001) and/or MEG recordings together with source analysis (Siegel et al., 2008) might offer an opportunity to arrive at a hierarchical model of the human brain, including uniquely human brain areas, by capitalizing on the functional hierarchy presented here.”

References

- Bastos, A. M., Vezoli, J., Bosman, C. A., Schoffelen, J. M., Oostenveld, R., Dowdall, J. R., ... & Fries, P. (2015). Visual areas exert feedforward and feedback influences through distinct frequency channels. Neuron, 85(2), 390-401.

- Seth, A. K., Barrett, A. B., & Barnett, L. (2015). Granger causality analysis in neuroscience and neuroimaging. Journal of Neuroscience, 35(8), 3293-3297.

- Mike X Cohen, https://www.youtube.com/watch?v=XqsSB_vpHLs

Thank you for listening!

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