Activity dependent development of maps in the visual system

Activity type

Sensory

- species
    - mammals
    - non-mammalian vertebrates
    - invertebrates
- ~~**ignore this Sensory literature for now** - too much literature for a 2000 word review limit?~~
    - *limit review to before vision onset?*
    - just do very brief overview in intro with statement that here we focus on intrinsic activity patterns in visual system and refer to other recent reviews?
- When?
    - Before eye opening and experienced visual patterns
        - Melanopsin
    - After eye opening
        - Hubel and Wiesel

Spontaneous

- What?
    - species
        - mammals
            - can occur before vision– long gestational timecourse
        - non-mammalian vertebrates
            - does not occur before vision– short gestation
    - patterns
        - in vitro
            - early development - before eye opening
                - retinal waves
                    - TODO: shatz, Wong, Feller work
                    - TODO: J. Zhou work
                - TODO: Subplate references, P. Kanold
                - Calcium waves– Konnerth, Moody, etc
            - after eye opening
                - TODO: Cossart visual cortex?
        - in vivo
            - early development - before eye opening
                - Rat

- Correlated bursting among RGCs [1]
- ‘Spindle bursts’
  - spindle shaped field potential oscillations in visual cortex [2]
- ‘Slow activity transients’
  - infra-slow LFP wave with nested fast oscillations
    - field oscillations and bursting multiunit activity in visual cortex [3]
      - 87% of L4 MUA occured during slow activity transients
      - extracellular recordings with glass electrode or multisite silicon probe
        - age P5-P7
          - peak frequency (8 - 31 Hz, mostly 18–30 Hz) and duration form single distribution (400 ms - 5 s), likely all continuous ‘spindle burst’ oscillations within the slow wave
        - age P9-P13
          - short duration events (<400 ms) first prominent around P9-P10 and increased frequency of these events until becoming the most common type by P13
          - very long duration (>5 s) encountered after P8 (‘splitting of events with maturation’)
          - two populations of events encountered:
            - long duration, beta band frequency (>5 s, 18–30 Hz)
            - short duration, alpha band frequency (<3 s, 10 Hz)
          - after P12 SATs less common and no longer dominant pattern– continuous cortical activity and slow wave sleep (delta)

- Mouse
  - retinal waves
    - Primary source of patterned activity throughout neonatal visual system [4]
    - Retinal input modulates synchronous calcium signals in cortical neurons [5]
      - they possibly recorded some retinal waves?
      - but most activity was independent of retinal input, and more likely ‘spindle bursts’
        - unknown if recordings were strictly from V1 or V2 (no method for identification)
        - calcium recordings were not summed population signals
      - *which might be same as the independent spontaneous V2 activity we saw* [4]
- Human
  - ‘Slow activity transients’
    - infra-slow LFP wave with nested fast oscillations
      - EEG field oscillations and bursting multiunit activity in visual cortex

[6][7]

        - around eye opening
            - Ferret
                - Correlated bursting activity among LGN and visual cortical neurons [8][9]
            - Rat
                - ‘Spindle bursts’
                    - field oscillations and bursting multiunit activity in visual cortex [3][7]
                - ‘Slow activity transients’
                    - infra-slow LFP wave with nested fast oscillations
                        - field oscillations and bursting multiunit activity in visual cortex [3][7]
        - ~~after eye opening~~
            - *too much literature in adult, limit review to before vision onset?*
                - monkey, cat, ferret, rodent, etc
            - patterned activity
                - Recent Konnerth peri-eye opening calcium imaging paper with direction selectivity?
                - intrinsic signal imaging
                    - Stryker work
                    - A. Grinvald work
                - multicell recordings
                - any mutlichannel recordings in newborn monkey (hubel wiesel just did single electrodes?)
                - ~~fast traveling waves~~
                    - adult (Y. Dan paper) [#Benucci:2007]

- Where?
    - Retina
        - Retinal waves propagate among RGCs [4]
    - LGN
        - Mouse
            - Spontaneous bursting among dLGN neurons sensitive to retinal input [10]
            - Inferred by matched retinal driven patterns in V1 and SC [4]
        - Ferret
            - Correlated retinal driven activity among LGN neurons [8]
                - multielectrode array recordings
                - neonatal, awake behaving ferret
                - recordings performed just before eye opening in ferret, around P21
                    - an age when spontaneous activity likely to be glutamatergic driven waves involving on-off bipolar cells and when retinotopic refinement and ODC formation complete
                - binocular correlations present
                    - they state it can’t be from retina, cause of statistical independence
                    - aspriating cortex (cortico-thalamic projections) abolishes the binocular correlation
                        - *but damage due to the ablation?*
                    - contralateral inputs drove LGN bursting more strongly than ipsilateral
                    - without retinal input, corticothalamic input necessary to sustain LGN neuron

bursting

- Superior colliculus
  - Retinal waves drive collicular neurons [4]
- Visual cortex
  - Mouse
    - Retinal waves propagate to cortical neurons [4]
    - Retinal input modulates synchronous calcium signals in cortical neurons [5]
  - Rat
    - Retinal input can drive spiking multiple unit activity in cortical neurons [2]
    - Retinal input can drive slow activity transients and spiking multiple unit activity in cortical neurons before and around eye opening [3]
  - Ferret
    - Correlated bursting among V1 neurons [9]
      - multielectrode array recordings
      - neonatal, awake behaving ferret
      - recordings performed just before eye opening in ferret, between P24-P29
        - an age when spontaneous activity likely to be glutamatergic driven waves involving on-off bipolar cells and when retinotopic refinement and ODC formation complete
  - Human
    - Slow activity transients in EEG signal in preterm human infants [6][7]

- When?
  - Before eye opening and experienced visual patterns
    - Before birth for some species
      - rabbit [11][12], monkey [13], human [6][7], cat [14]
    - After birth for some species
      - rodent [4][2][3], rabbit [11][12], ferret [14][15][16][8][9]
  - ~~After eye opening~~
    - experiential pattern replay/dreams
      - analogs to hippocampal - place cell replays (Wilson work) for learning and memory?
      - Y. Dan visual pattern replay paper
      - standing waves and fast travelling waves [#Benucci:2007]
- Why?
  - activity dependent circuit establishment and refinement– lessons from other systems
    - cite R. Wong review
    - *short blurb on other systems*
    - chick neuromuscular junction (lichtmann sanes)
    - spontaneous motor circuit activity V. Hamburger & (Petterssen Nature paper)
  - activity dependent visual map development
    - anatomical - structural
      - axon growth
        - xenopus, zebrafish literature?
        - LGN and SC
          - rodent
            - mouse

            - TODO: beta2 nAchR ko mouse?
            - TODO: N. Spitzer reference on activity-dep Ca2+ growth *Cortex
        - Ruthazer and Olavarria paper
- axon refinement
    - xenopus, zebrafish literature?
    - LGN and SC
        - rodent
            - mouse
                - Retinocollicular axon - retinotopic map refinement requires cholinergic retinal waves [17]
                    - beta2 nAchR ko mice, focal DiI tracer injections into retina
                - beta2 nAchR ko and transgenic mice show that nAChR mediated spontaneous activity in the retina is essential for retinotopic map refinement, eye specific segregation [18]
                - RGC refinement and deficits in beta2 nAchR ko occurs at the level of single RGCs [19]
    - cortex
        - cortico-collicular axon arborizations [20].
            - Nice DiI reconstructions of cortico-collicular axons in rat
        - Ruthazer and Olavarria paper
- dendrite growth?
    - cortico-collicular recepient cells in SC,
        - Recent constantine-paton paper [20].
            - Cortico-collicular axons needed for ‘caliber 3’ dendritic filopodia density.
            - Eye opening regulates spine density in ‘caliber 3’ dendrites
    - Golgi or DiI analysis in ferret, cat, monkey, or rodent cortex?
        - Ruthazer and Olavarria paper
    - Golgi or DiI analysis in LGN or SC?
- dendritic refinement
    - spine dynamics?
        - TODO: xenopus literature?, H. Cline
- cell migration
    - rodent
        - cortex
            - interneurons
                - TODO: recent Fishell paper
                - TODO: recent ZJ Huang papers
                - TODO: Ben-Ari, JB Manent activity dependent interneuron migration in vitro model
    - higher mammals
        - cortex
            - retinal wave evidence in macaque monkey retina in vitro [13]
                - occurs as early as E60, before start of eye specific segregation
                - macaque monkey neocortical neurogenesis (E40, SP/L6), (E56 – E100, L5 – L2/3)

            - *unknown, but due to gestational timing, waves likely to have greater influence on cell migration and cortical patterning than in lower mammals*
                - both excitatory and inhibitory cell migration overlaps significantly with the period for retinal waves

- functional - physiological
    - synapse maturation
        - retinocollicular synapse
            - Increased AMPA/NMDA ratios and AMPA quantal amplitudes during first postnatal week [21]
            - burst activation in vitro capable of inducing LTP [21]
            - delayed maturation and greater LTP at beta2-/- nAchR ko synapses [21]
    - retinotopy
        - Retinotopic map refinement requires retinal waves in SC [17]
            - beta2 nAchR ko mice, focal DiI tracer injections into retina
            - preferential anatomical terminal zone elongation along nasal-temporal axis
        - Disrupted retinotopic map in beta2 nAchR ko mice in LGN (first order connections) [22]
            - using tungsten microelectrode extracellular recordings
            - physiological receptive fields preferentially disrupted (elongated) along nasal-temporal (visual field azimuth) axis
            - Abnormal segregation of on- and off-centered cells in LGN that is not seen in wt
                - *precocious glutamate bipolar cell mediated waves?*
        - Altered retinotopic map in beta2 nAchR ko mice in SC (first order connections) [23]
            - using tungsten microelectrode extracellular recordings
            - physiological receptive fields elongated along nasal-temporal axis
        - Altered retinotopic map in beta2 nAChR-/- mice in SC (first order connections) [24]
            - using instrinsic signal imaging
            - retinotopic map preferentially disrupted (elongated) along anterior-posterior (nasal-temporal) axis of SC
        - Altered retinotopic map in beta2 nAchR -/- mice in V1 (second order connections) [25]
            - Intrinsic signal imaging of mouse V1 for visual space map
            - Extracellular microelectrode recordings for single cell receptive fields
            - Preferential disruption (elongation, scatter, response amplitude) along the visual space azimuth (nasal-temporal axis)
            - They speculate that waves regulate ephrinA gradients to explain the nasal-temporal disruption since travelling waves had not been found to have a preferred direction at the time
        - Cortico-collicular alignment of retinotopy (quaternary order connections, L5 –> SC) [26]
            - Transgenic mice, tracer injections, intrinsic signal functional mapping
            - Used ephA3ki/ki (knock in) mice crossed with beta2 nAchR -/- mice for the crucial experiment in Figure 6.
            - These mice have duplicated retinocollicular map, but only a single, non-matched corticocollicular projection when no cholinergic waves are present.
    - eye specific segregation
    - ocular dominance columns
        - development of ODCs in ferret [27]

                - epibatidine injections and tracer injections
                - ocular dominance bias index with extracellular microelectrode recordings
                - spontaneous cholinergic activity in retina required for cortical ODC formation
            - TODO: Crair, Stryker
        - orientation selectivity
            - TODO: Crair, Stryker
            - TODO: Recent Fitzpatrick work
            - TODO: ongoing J. Cang unpublished work? (look at abstr from SFN, our CSHL conf last year)
        - direction selectivity
            - TODO: Recent Konnerth peri-eye opening calcium imaging paper
            - TODO: Recent Fitzpatrick work (the reprogramming of selectivity)
- How?
    - Permissive
        - Spatiotemporal pattern does not matter
            - Perhaps just absolute levels of activity needed?
            - homeostasis, celluar growth and survival?
    - Informative
        - Spatiotemporal pattern does matter
            - Temporal activity pattern
                - Time scale
                    - eye-specific segregation
                        - before eye opening
                            - Synchronous activation of RGCs in both eyes with ChR2 disrupts eye-specific segregation in SC and LGN [28]
                            - Relevant window for spike timing differences of RGCs in both eyes within 100s of milliseconds [28]
                                - chR2 stimulation of RGCs, anatomical segregation analysis in SC
                - Mechanism
                    - Coincident pre-post synaptic activity - Hebbian plasticity
                        - Dependent on NMDA-R?
                            - maybe yes?
                                - TODO:
                                - HP Xu recent work?
                            - maybe not?
                                - LTD independent of NMDA-R activation in mouse [29]
                                    - in vitro explant with extracellar field potentials and high freq stim to mimic retinal waves
                                    - bidirectional maturation
                                        - finds LTD early between birth and eye opening
                                        - finds LTP after eye opening through critical period

                    - cites [#Butts:2007] for bidirectional synaptic strength changes in single LGN cells
                - L-type calcium channel plateau potentials at developing LGN neurons [#Lo:2002]
                - retinogeniculate PSC bursting is independent of NMDAR activation (NMDAR1 ko mice, ex vivo, extracellular)[10]
                - HP Xu recent work?
        - Independent of NMDA-R?
            - endocannabinoid induced LTD?
                - but this type of activation still requires NMDA activation? [30]
                    - this type of coincidence detection reviewed elsewhere [30]
            - mGluR-VSCC-IP3R-eCB coincidence detector [31]
                - this form of LTD independent of postsynaptic NMDA receptors
                - utilizes metabotropic glutamate receptors, voltage sensitive calcium channels, IP3 stores, and endocannabinoid receptors
                - detects firing coincidence at 125 ms time scale (*versus 25 ms time scale for NMDA dependent LTP*)
                - described at L4 to L2/3 synapses in somatosensory cortex
            - bistable switch in spike statistics for postsynaptic neurons?
                - critical level of coincident presynaptic activity needed to cause spike?
                    - during early development?
                        - biophysical membrane and cable properties different in immature neurons
                            - more voltage gated calcium conductance
                            - less sodium channels
                        - lower fidelity spike transmission initially?
    - Non-coincident – alternate, lagged timing based plasticity rule?
- Spatial activity pattern
    - Unknown: no direct experiment yet
        - experiment needed: to control spatio-temporal activity patterns before start of vision
            - Analagous to the classic Sensory activation experiments
                - owl prism experiments Knudsen
                - cat goggle experiments
    - Instructive role of spatial activation hinted at by Hong-Ping's paper? [18]

        - Necessitates the temporal activity mechanisms with an additional spatial dimension via a wavefront
        - Spatial patterns setup in periphery (RGCs) and communicated across levels of visual organization [4]
    - Spatiotemporal information in retinal waves TODO: make table of these properties?
        - *Perform quick analysis of wavefront size within our in vivo waves dataset and include as a new data in a Figure?*
        - Wave speed from in vitro and in vivo literature consistent (100s of microns/sec)
            - retina in vitro (100 - 500 μm/s; mouse, rabbit, ferret, monkey) TODO: zhou, feller, feldheim, chalupa papers
            - SC in vivo (28 - 60 μm/s = 90 - 180 μm/s in retina with 3x scale factor) [4]
        - Wave size (wave area) smaller within in vitro literature [32] and bigger in vivo [4]
            - Wave propagation failure in vitro because of some combination of in vitro conditions such as bath medium, temperature, and cut connections?
        - Wave direction along VT - DN axis in vitro [32] and in vivo [4]
            - This makes the wavefront axis perpindicular to preferred axis for activity mediated refinement

Figure: Schematic of visual cortex primary and secondary areas, pathway illustration, and summary of retinal influence? (incl Olavarria work?)

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