

# Activity dependent development of maps in the visual system

Our focus will be on activity-dependent development in the visual system before vision. See recent reviews for coverage of the molecular mechanisms underlying visual map development [1].

Cang and Feldheim Ann Rev Neurosci 2013 review [1]:

- Fig1 Schematic of multimap alignment (somatosensory, visual) in SC
- Fig2 Schematic of ephrinA/ephA countergradients in the retina, LGN, SC, and V1
- Fig3 Schematic of retinotopy study methods– focal Dil injections and intrinsic signal imaging
- Fig4 Schematic of binocular alignment of retinotopy, ipsi and contra reversed N-T axis targeting for visuotopy and center out ephA gradients
  - center out gradient (proposed by Sperry 1963) found for ephA found in developing retinas of human and ferrets ([#Huberman:2005]; Lambot2005)
  - difficult to demonstrate in mice because of small number of RGCs projecting ipsilaterally (but Feldheim2000, Fig6c indicates it may infact be there)
- Binocular matching of orientation tuning
  - Hubel and Wiesel 1962, single cortical neurons are binocular yet selective for stimulus orientation and tuned to similar orientation through both eyes
  - in carnivores and primates neurons with similar orientation preferences organized into columns (Hubel and Wiesel 1962; Grinvald 1986; Blasdel 1986)
  - ...and the maps of orientation columns are binocularly matched [2]
  - Two models?
    - Hubel and Wiesel 1962 feed forward model
      - orientation selectivity arises from arrangement of geniculate inputs and each neurons' preference determined by layout of elongated ON and OFF subregions in their receptive field
    - Feed back models
      - orientation selectivity is an emergent property of intracortical circuitry (Adorjan 1999; Ben-Yishai 1997; Somers 1995)
  - Development
    - orientation selectivity develops after retinotopic mapping and eye specific segregation in dLGN and matures after eye opening ([3] [#Huberman:2008a])
      - mice have no orientation columns but id. V1 neurons are highly selective [#Niell:2008] and prefer matched orientations through both eyes ([#Wang:2010b]; [4])
      - binocular matching of orientation preference depends on vision in mice [4], but significant ON-OFF subregion binocular correspondence exists independent of visual experience [4]

## 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
      - slow time course melanoma activation of ipRGCs in rodent before eye opening S. Hattar work, other j. Hopkins and brown univ work
  - 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
          - Occur in all amniote species examined (turtle, chicken, rodent, rabbit, ferret, cat) [5], including monkey [6]
            - chicken [#Wong:1998][#Catsicas:1998]
            - turtle [#Sernagor:1996]
            - ferret [7][8][9]
            - cat [7]
            - rabbit [10]
            - mouse [11][#Bansal:2000]
            - monkey [6]
          - Do not occur in amphibians [12]
            - Xenopus laevis tadpoles wildtype and albino
            - Microelectrode array recordings
            - Visually evoked responses as soon as RGCs innervate targets (unlike mammals)
            - Authors conclude that the two branches of tetrapods (amphibians and amniotes), evolved different strategies to mediate activity-dependent development during visual system formation
        - Subplate –
          - Subplate neurons are likely key to relaying oscillatory activity to developing cortical neurons Kanold and Luhmann review [13] *Nice Ann Rev Neuosci review*

with summary table of references for species, cortical area, neurotransmitter, etc)

- SPn removal in visual cortex prevents thalamocortical synapse maturation, maturation of inhibition in L4, development of orientation selectivity, and formation of ODCs [13]
- physiology evidence for activity relay in vitro and in vivo in somatosensory cortex
- physiology evidence for activity relay in vitro cat visual cortex (old disynaptic response Friauf&Shatz 1991 paper, possibly Hanganu 2001, 2002, and Hirsch & Luhmann 2008)
- Ghosh/Kanold/Shatz subplate kainic acid excitotoxicity or immunotoxin work in cats suggests that subplate cells play a key role in ocular dominance column formation, but not known if this role is activity-dependent  
[#Ghosh:1990][#Ghosh:1992][#Kanold:2003]
  - ~~P. Kanold~~ *No one knows if subplate cells in occipital cortex exhibit spontaneous activity during development*
  - Only subplate cells in somatosensory cortex have been checked for spontaneous activity (Luhmann, Hanganu, also Kanold JNS 2012 work)  
[#Hanganu:2001][#Hanganu:2002][#Dupont:2006][#Kanold:2006][#Tolner:2012]
- Calcium waves
  - have been observed in several areas of rodent lateral and medial entorhinal cortex, temporal cortex, and fronto-parietal cortex, but none of the following groups (Konnerth, Peinado, Moody, Yuste/Ikegaya) has checked occipital cortex before eye opening:
    - ~~[#Garaschuk:2000], [#Peinado:2000], [#Corlew:2004], [#Namiki:2013]~~  
*None of these groups has done occipital cortex in vitro*
- after eye opening
  - UP-DOWN states in mouse visual cortex [14]
    - P14-P21 C57/BL6 brain slices
    - multicellular two-photon calcium imaging with Fura2 and patch clamp recordings
    - all cortical layers 2–5 imaged
    - average interval of synchronous population events was  $55 \pm 4$  s (peak synchrony in histograms, considerably slower than slow oscillations of 0.1 - 0.5 Hz)
- in vivo
  - early development - before eye opening
    - Rat
      - Correlated bursting among RGCs [15]
      - ‘Spindle bursts’
        - spindle shaped field potential oscillations in visual cortex [16]
      - ‘Slow activity transients’
        - infra-slow LFP wave with nested fast oscillations
          - field oscillations and bursting multiunit activity in visual cortex [17]
            - 87% of L4 MUA occurred 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 [\[18\]](#)
    - Retinal input modulates synchronous calcium signals in cortical neurons [\[19\]](#)
      - 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* [\[18\]](#)
- Human
  - ‘Slow activity transients’
    - infra-slow LFP wave with nested fast oscillations
      - EEG field oscillations and bursting multiunit activity in visual cortex [\[20\]\[21\]](#)
- around eye opening
  - Ferret
    - Correlated bursting activity among LGN and visual cortical neurons [\[22\]\[23\]](#)
  - Rat
    - ‘Spindle bursts’
      - field oscillations and bursting multiunit activity in visual cortex [\[17\]\[21\]](#)
    - ‘Slow activity transients’
      - infra-slow LFP wave with nested fast oscillations

- field oscillations and bursting multiunit activity in visual cortex [17][21]

- ~~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 multichannel 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 [18]
- LGN
  - Mouse
    - Spontaneous bursting among dLGN neurons sensitive to retinal input [11]
    - Inferred by matched retinal driven patterns in V1 and SC [18]
  - Ferret
    - Correlated retinal driven activity among LGN neurons [22]
      - 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
      - aspirating 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 [18]
- Visual cortex
  - Mouse
    - Retinal waves propagate to cortical neurons [18]
    - Retinal input modulates synchronous calcium signals in cortical neurons [19]
  - Rat

- Retinal input can drive spiking multiple unit activity in cortical neurons [16]
  - Retinal input can drive slow activity transients and spiking multiple unit activity in cortical neurons before and around eye opening [17]
- Ferret
  - Correlated bursting among V1 neurons [23]
    - 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 [20][21]
- When?
  - Before eye opening and experienced visual patterns
    - Before birth for some species
      - rabbit [10][24], monkey [6], human [20][21], cat [7]
    - After birth for some species
      - rodent [18][16][17], rabbit [10][24], ferret [7][8][9][22][23]
  - ~~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 Ca<sup>2+</sup> 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 [25]
    - beta2 nAChR ko mice, focal Dil 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 [26]
  - RGC refinement and deficits in beta2 nAChR ko occurs at the level of single RGCs [27]
- cortex
  - cortico-collicular axon arborizations [28].
    - Nice Dil reconstructions of cortico-collicular axons in rat
  - Ruthazer and Olavarria paper
- dendrite growth?
  - cortico-collicular recipient cells in SC,
    - Recent constantine-paton paper [28].
      - Cortico-collicular axons needed for 'caliber 3' dendritic filopodia density.
      - Eye opening regulates spine density in 'caliber 3' dendrites
  - Golgi or Dil analysis in ferret, cat, monkey, or rodent cortex?
    - Ruthazer and Olavarria paper
  - Golgi or Dil 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 [6]
        - 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 and length of development, 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 [29]
  - burst activation in vitro capable of inducing LTP [29]
  - delayed maturation and greater LTP at beta2-/- nAChR ko synapses [29]
- retinotopy
  - Retinotopic map refinement requires retinal waves in SC [25]
    - beta2 nAChR ko mice, focal Dil 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) [30]
    - 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) [31]
    - 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) [32]
    - using intrinsic 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) [33]
    - 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) [34]
    - 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 [35]
    - epibatidine injections and tracer injections
    - ocular dominance bias index with extracellular microelectrode recordings
    - spontaneous cholinergic activity in retina required for cortical ODC formation
  - ODC and orientation selectivity maps in cat independent of visual experience [2]
- orientation selectivity
  - ODC and orientation selectivity maps in cat independent of visual experience [2]
  - TODO: Recent Fitzpatrick work?
  - Orientation selectivity develops after retinotopic mapping and eye specific segregation in dLGN and matures after eye opening (see recent reviews [3] and [Huberman:2008a])



- Mice have no orientation columns but individual V1 neurons are highly selective [#Niell:2008] and prefer matched orientations through both eyes ([#Wang:2010b]; [4])
- Binocular matching of orientation preference depends on vision in mice [4], but significant ON-OFF subregion binocular correspondence develops completely independent of visual experience [4]
  - adult mice either normally reared or dark reared from birth or P11. single unit recordings (FHC high impedance tungsten) in V1 under urethane anesthesia. Spike triggered averaging (STA) with sinusoidal gratings. Also did flashed spots and PSTH analysis, same results.
  - Fig 5 nice model showing how subregion correspondence gives rise to binocular matching positive or negative sign overlap and their results fit the positive sign overlap model for binocular matching
  - Fig 6 shows subregion correspondence in absence of any light exposure
    - distribution of binocular differences in RF orientation not uniformly distributed, even with DR (also no difference between DR0 DR11, thus any melanopsin not important for orientation maps) and centered around 0° difference
    - large scale orientation maps and matching experience-independent [2] and develops in absence of coordinated binocular activity [#Godecke:1996]
- direction selectivity
  - Recent Konnerth peri-eye opening calcium imaging paper [36]
    - calcium imaging in vivo
    - L2/3 neurons mouse visual cortex
    - early direction selectivity in orientation selective cells independent of visual experience
    - unmodified by dark rearing
    - authors conclude dev dir sel distinctly different in mice from ferrets
  - TODO: Recent Fitzpatrick work (the reprogramming of selectivity)
- How?
  - Permissive
    - Spatiotemporal pattern does not matter
      - Perhaps just absolute levels of activity needed?
      - homeostasis, cellular 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 [37]
              - Relevant window for spike timing differences of RGCs in both eyes within 100s of milliseconds [37]
                - chR2 stimulation of RGCs, anatomical segregation analysis in SC

- Mechanism
  - Coincident pre-post synaptic activity - Hebbian plasticity
    - Dependent on NMDA-R?
      - maybe yes?
        - TODO: Constatine-paton, Colonnese elvax SC experiments
        - HP Xu recent work?
      - maybe not?
        - LTD independent of NMDA-R activation in mouse [\[38\]](#)
          - in vitro explant with extracellular 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 postsynaptic currents (periodic barrages of activity) is independent of NMDAR activation (NMDAR1 ko mice, ex vivo, extracellular)[\[11\]](#)
        - HP Xu recent work?
    - Independent of NMDA-R?
      - endocannabinoid induced LTD?
        - but this type of activation still requires NMDA activation? [\[39\]](#)
          - this type of coincidence detection reviewed elsewhere [\[39\]](#)
      - mGluR-VSCC-IP3R-eCB coincidence detector [\[40\]](#)
        - 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
        - Analogous 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? [\[26\]](#)
      - 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 [\[18\]](#)
    - 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  $\mu\text{m/s}$ ; mouse, rabbit, ferret, monkey) TODO: zhou, feller, feldheim, chalupa papers
        - SC in vivo (28 - 60  $\mu\text{m/s}$  = 90 - 180  $\mu\text{m/s}$  in retina with 3x scale factor) [\[18\]](#)
      - Wave size (wave area) smaller within in vitro literature [\[41\]](#) and bigger in vivo [\[18\]](#)
        - 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 [\[41\]](#) and in vivo [\[18\]](#)
        - This makes the wavefront axis perpendicular 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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