Outline for both lectures this week:
I. The big questions and why they matter and a few bare basics of brain development
II. Three Test Cases of behavioral and neural development
   A. Face perception and the FFA
      A Long sidebar about the role of connectivity
   B. The Visual Word Form Area
   C. The navigation network and reorientation
III. Could brain organization be different if:
   A. Reorganization after brain damage
   B. Very different input (e.g., blindness)

Brief recap of last lecture:
What if anything is Innate about Face Perception?

Maybe not that much!

• Bias to look at faces (though a very simple template might suffice).
• Good face discrimination in newborns, and face-deprived monkeys but maybe not based on face specific mechanisms?
• Face patches apparently require experience to develop.

But: How do they know to always arise right here?

Deep net modeling can inform these questions by asking:

What do you need to build in to a system to get face patches?
What experience is necessary to produce face patches in a deep net?
And why computationally do we have them in the first place?
Structural Connectivity from Diffusion Tractography

Principle: Restricted Diffusion of Water in Axon Bundles

Diffusion MRI discovers orientations of diffusion at each point in brain.

Tractography follows these vectors to reconstruct structural connections.

Works well to discover big fiber bundles. Discovers some smaller connections but highly fallible. The best method for discovering connectivity in humans. So we can use it to ask: Is the FFA distinct from its neighbors in connectivity?
Do Connectivity Fingerprints Predict Function in Adults?

For each voxel:
Find its connectivity:

To each of a set of anatomical regions:

This is the “connectivity fingerprint” of that voxel (Saygin et al 2012).

Now ask:
Can we predict function of that voxel from its connectivity?
e.g., Is the FFA distinct from its neighbors in connectivity?
Do Connectivity Fingerprints Predict Function in Adults?

Can we predict function of that voxel from its connectivity? **Yes!**

Is the FFA distinct from its neighbors in connectivity? **Yes!**

Saygin, Osher, others, 2012, 2016

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Do Connectivity Fingerprints Predict Function in Adults?

This is in adults. Recall that most long-range connectons are present at birth. So, might this connectivity play a role in development? This brings us to.....

Can we predict function of that voxel from its connectivity? Yes! All these regions have distinct connectivity fingerprints!

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Rewired Ferrets!
what?

Redirect connections via surgery at birth.


Question: Does connectivity “instruct” functional development?
Redirect connections via surgery at birth.
Now primary auditory cortex (A1) is getting visual input.
If input were sufficient to determine the function of a region of cortex, we should find that A1 now takes on the function of V1! What do you think will happen?
Rewired Ferrets!

A1 responds to visual input. Get orientation columns!

When these neurons are active, Does the ferret *see* or *hear*? (train with nonrewired input to report on sound versus light).

Now primary auditory cortex (A1) is getting visual input. If input were sufficient to determine the function of a region of cortex, we should find that A1 now takes on the function of V1! What do you think will happen?
Rewired Ferrets!

A1 responds to visual input. Get orientation columns!

When these neurons are active, Does the ferret see or hear? (train with nonrewired input to report on sound versus light).

Rewired ferrets see neural responses in A1. So, this region is “instructed” by visual input to become visual cortex. So, experience & connectivity both determine cortical function!

But this is a ferret! What about humans?

Ferret photo & figures © sources unknown. This content is excluded from our Creative Commons license, see https://ocw.mit.edu/fairuse.
Does Cortical Function Depend on Experience in Humans? And does Connectivity Matter?

Are there any cortical regions in humans whose selectivity *must* be due to experience?

Consider the case of visual words and letters:

Humans have only been reading for a few 1,000 years. Not long enough for natural selection to have crafted innate machinery for reading. So, if we have specialized cortical machinery for perceiving letters/words, it must be wired up by experience. Do we? How would we find out?

Experience & connectivity both determine cortical function! But this is a *ferret*! What about humans?
A small region in the left hemisphere shows higher activation for words than line drawings:

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Does Cortical Function Depend on Experience in Humans? And does Connectivity Matter?

Are there any cortical regions in humans whose selectivity must be due to experience?

If we have specialized cortical machinery for perceiving letters/words, it must be wired up by experience. Do we? YES!

The “visual word form area” or VWFA

Is the location of this region determined by connectivity?
Can we predict the location of the VWFA at age 8 from connectivity fingerprint at age 5, before the region arises?

Saygin et al 2016
Taking Stock

• Basic structure of brain is innate: most neurons and long-range connections present at birth.

• Selective cortical regions appear to depend on experience. Face-deprived monkeys do not have face patches. Ferrets “see” response of A1 rewired with visual input. VWFA cannot be innate, yet arises in consistent location possibly instructed by innate long-range connectivity.

• So is it all over for Kant and his “a priori conditions” of cognition? “Space . . . can be given prior to all actual perceptions, and so exist in the mind a priori, and . . . can contain, prior to all experience, principles which determine the relations of these objects.”

• Let’s get back to representations of space…. 
Are Representations of Space Innate?

**Question:** Are some aspects of the cognitive map system present prior to an animal’s experience with the world?

Record from spatial cell types in infant rats when they first open their eyes and leave the nest (end of 2\textsuperscript{nd} week):

- HD cells appear at P12 BEFORE eye opening & spatial exploration, place & border cells soon thereafter.
- Suggests: System for representing space is largely innate. Just like Kant proposed in the 1700s!

What about reorientation?
Reorientation and The “Geometric Module”

Cheng & Gallistel (1986)

(a) [Diagram]

(b) [Diagram]

Hermer & Spelke (94)

• Same result for 18 - 24 month old infants.
• Same result for adults when performing a verbal shadowing task.

Idea

• “Geometric Module” uses ONLY spatial layout to orient animal/baby in environment
• Evolutionary rationale: Layout of environment is unchanging, colors, odors, etc. are not

Question: Is this reorientation system innate? How would you tell?
Controlled Rearing!

Challenge:
Hard to test a behavioral ability (like reorientation) at birth. Yet if you wait until later, then you don’t know if the relevant behavioral ability was innate or learned.
A pickle.
But there is a way around this, and it is called…..

Controlled Rearing: Raise an animal without the relevant experience, then ask if the ability arises anyway.
Example…..

Question: Is this reorientation system innate?
How would you tell?
Controlled Rearing!

Use of geometric (shape) cues to reorient:

Get fertilized eggs from local hatchery.
Incubate eggs until hatching in darkness.
Rear for 3 days in rectangular or circular cage.
Hang red plastic object in middle of cage;
Chicks imprint.
Over 3 trials, chicks see “mom” disappear behind panel and are allowed to rejoin.
Then use the classic reorientation test…

Question: Is this reorientation system innate?
How would you tell?
1. Place chick in cylindrical grid in rectangular box.
2. Hide “mom” behind one of blue panels.
3. Lower opaque cylinder around chick and grid.
4. Rotate box 90 degrees.
5. Raise both cylinders and allow chick to look for mom.
6. Tally which corner s/he goes to.
7. Repeat for 16 trials.
8. Give chick back to hatchery.

Experiment 2: raise in total darkness until test. Same result.

Question: Is this reorientation system innate?  
YES! Go, Kant!

No geometric experience necessary to use geometry to reorient.
Recap: What Cortical Selectivities are Innate?

The Face System:
Maybe not that much!
• Bias to look at faces (though a very simple template might suffice).
• Good face discrimination in newborns, and face-deprived monkeys but maybe not based on face specific mechanisms?
• Face patches apparently require experience to develop.

Role of Connectivity in Cortical Development:
• Most long-range connectivity is present at birth.
• Connectivity can causally affect function of a cortical region (ferrets).
• Category-selective regions have distinctive connectivity.
• Connectivity predicts location of VWFA.

VWFA: One region whose selectivity of VWFA can not be innate.

The space system:
• HD cells arise before exploration, place and border cells soon after.
• Chicks reorientation to the geometry of space despite no prior experience.
• Kant was right about space being a priori!
Lecture 11: Development

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Plasticity: Can the Brain Reorganize after Damage?

**Language System (best studied):**
- Damage to these regions in adulthood leads to lasting language deficits.
- Damage in first few months of life > very good language (not perfect), reorganization to RH.
- Damage after age 5: outcome not good, no reorganization to RH.

So: the compensatory potential of the right hemisphere might already be limited at the age of 5 years.

**Kennard Principle:**
"if you are going to have brain damage, have it early."
Does not always hold….

**Hebb Principle:**
It depends!
Like building a house, there is a necessary sequence in development. If the foundation is not built you cannot build the first floor. Similarly, early deficit in hearing could produce bigger deficits in language.

What about regions in visual cortex?
Cortical Regions Specialized for Processing:
Shape, Color, Motion, Faces, Places, Bodies & Words

Consequence of lesion in adulthood? not much recovery
In childhood?

Damage to these regions produce
achromatopsia
agnosia
akinetopsia
prosopagnosia
topographic disorientation
alexia
Is the Cortical Site of the FFA Already Determined at Birth?

Patient Adam: damage to bilateral occipital and occipitotemporal cortex at one day of age (stroke). tested at age 16.

Acuity is not great, and object recognition is not perfect, but he can recognize common objects from photos (87% correct) and line drawings (58%; for nonliving things, 75% correct).

But: Profound prosopagnosia. Failure to recognize any Baywatch characters despite spending 1 hour per day watching it for 1.5 years.

Suggests: the relevant brain region for faces is already specified at birth.

This kind of evidence could be informative, in principle. But damage is broad, behavioral tasks not matched for difficulty, etc.

More data are needed to answer this important question.
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Functional Organization in Congenital Blindness

What does V1 do?
- fMRI: language activates V1
- TMS: causal role in language processing
- Pretty radical, it is hard to think of more different functions than low-level vision and language.

FFA, EBA, VWFA, PPA?
- Many claims that these regions can be activated by touching relevant stimuli recoded images with “sensory substitution”
- But I promised one more contradictory bit of data and here it comes…..
Development of visual category selectivity in ventral visual cortex does not require visual experience

Job van den Hurk\textsuperscript{a,b,1}, Marc Van Baelen\textsuperscript{a,c}, and Hans P. Op de Beeck\textsuperscript{a}

Scan Congenitally Blind subjects
While they hear sounds associated w/ faces, bodies, objects, scenes:

- **face**: laughing, chewing, blowing a kiss, whistling
- **body parts**: scratching, hand clapping, finger snapping, bare foot steps, knuckle cracking
- **objects**: car starting, washing machine, bouncing ball, fluid pouring into glass, ripping of paper
- **scenes**: waves crashing on a beach, calm lake, crowded restaurant, train station, busy road

Do we see activation in FFA, PPA, for preferred category?
Development of visual category selectivity in ventral visual cortex does not require visual experience

Job van den Hurka,b,1, Marc Van Baelena,c, and Hans P. Op de Beecka

Scan Congenitally Blind subjects
While they hear sounds associated w/ faces, bodies, objects, scenes:

Would face-deprived monkeys show similar auditory responses?
Do these reflect connectivity?

Do we see activation in FFA, PPA, for preferred category?

Yes, similar topography of response for each category for auditory blind and visual sighted, indicating that:

But then what about the paper on face-deprived monkeys?

Seeing faces is necessary for face-domain formation

Michael J Arcaro1,2, Peter F Schade1,2id, Justin L Vincent1, Carlos R Ponce1id & Margaret S Livingstone1,2id

Welcome to the cutting edge!