space and time in the brain – cogs260 – cogs177 – Nitz – winter, 2011

week 2 – egocentric mapping, parietal cortex, personal space
hemi-neglect following right parietal cortex injury

**graded** lack of responsiveness to stimuli presented to L side of body or to L side of visual field (contrast with sharp cutoff with, for example, occipital cortex injury)

lack of responsiveness is **multimodal** - pertains to tactile, visual, and auditory stimuli as well as to motor movements (e.g., the position of a hand movement’s goal)

lack of responsiveness to stimuli on L side is exacerbated by **competition/attention** with simultaneous stimuli on R side (competition applies across sensory modalities)

**postural dependence** - improved responsiveness to L side stimuli when head or eyes are directed to R of body or if stimulation of proprioceptive neurons mimic such postural changes

**laterality** – hemineglect is heavily biased toward R-parietal lesions with L-field neglect as opposed to L-parietal lesions with R-field neglect
parietal cortex contains a ‘mental map’ across which the positioning of items in the environment are distributed

parietal cortex is the end-point for the ‘where’ pathway for visual processing

parietal cortex is an ‘association area’ in that it receives sensory input of many types: auditory, visual, proprioceptive, vestibular, somatosensory

parietal cortex sends output to both sensory, motor, premotor, and prefrontal cortex
some potential explanations for features of hemi-neglect

lack of responsiveness is multimodal - pertains to tactile, visual, and auditory stimuli as well as to motor movements (e.g., the position of a hand movement’s goal)

parietal cortex sub-regions are most often sensitive to more than one sensory modality (e.g., VIP sensitive to tactile, visual, vestibular stimuli, LIP sensitive to visual and auditory stimuli, PPR sensitive to visual and auditory stimuli as they relate to hand movements)
early Mountcastle data showing that position-specific responses of parietal neurons to visual stimuli are strongly modulated by attention:

in the ‘no-task’ mode, a monkey fixates a central cross while a visual stimulus is placed within the preferred visual field of a recorded neuron – the neuron responds to the stimulus, but only weakly

in ‘task’ modes A and B, the monkey must monitor the stimulus placed in the visual field to detect when it dims - the neuron’s response to the same stimulus when attended is much stronger

thus, the neuron is simultaneously sensitive to the spatial position of a stimulus and to the degree to which that position requires attention

if our perception of restricted parts of the available visual field is determined by which neurons (and their associated response fields) are most active, then the attention effects here may explain the impact of competition on neglect
Hemi-neglect following right parietal cortex injury

Lack of responsiveness to stimuli on L side is exacerbated by competition with simultaneous stimuli on R side (competition applies across sensory modalities).

Parietal responses to visual stimuli are strongly dependent on salience as shown in this figure from Gottlieb et al. (Nature, 1998) where the response to a visual stimulus within the cell's receptive field (gray areas) depends on whether that stimulus matches one given during the cue period.

Thus, the presence of a right field visual stimulus in a hemi-neglect patient may attain salience (be attended to) over another visual stimulus within the L visual field.

In this case, the responses of those few L parietal neurons sensitive to L visual field stimuli may be non-existent.

Note that this also means that what doesn’t register in the form of neural activity in the parietal cortex does not register perceptually.
in studies of monkey parietal cortex, the response field of a large number of neurons has been determined (i.e., that part of the visual field where presentation of a stimulus produces maximal response)

from such work, we obtain the graph to the right where the number of neurons most sensitive to different parts of the visual field is depicted.

three features: 1) the curve is not flat, meaning that more neurons are devoted to some regions of the visual field than others; 2) the curve does not peak at zero (center of the visual field); 3) the curve is graded with respect to L vs. R visual fields (i.e., there is no sharp cutoff for L vs R-field responsiveness for R vs. L parietal cortices)

this may begin to help us understand why hemineglect is graded in nature and suggests a scenario that may explain why hemineglect is largely limited to R-parietal-lesions with L-field neglect
some potential explanations for features of hemi-neglect

graded lack of responsiveness to stimuli presented to L side of body or to L side of visual field (contrast with sharp cutoff with, for example, occipital cortex injury)

why the neglect only of L side with R parietal lesions and not vice versa? – why graded?

in monkeys, for whom right parietal lesions do not produce hemi-neglect, L and R parietal neuron populations respond mainly to R- and L-visual field stimuli (respectively), but a small population in each hemisphere responds to stimuli in the ipsilateral visual field.

in humans, it is possible (and some EEG studies agree) that R parietal cortex is sensitive to L and R visual fields, but L parietal cortex is sensitive only to the R visual field.
hemi-neglect following right parietal cortex injury

**postural dependence** - improved responsiveness to L side stimuli when head or eyes are directed to R of body or if stimulation of proprioceptive neurons mimic such postural changes

answers lie in defining parietal cortex receptive fields, spatial frames of reference, and...gain fields?
different combinations of head and eye positions are yield a set of gaze angles relative to the body

neurons of parietal cortex sub-region LIP are recorded – the preferred direction of saccades elicited by visual stimuli is determined – firing rates in response to stimuli eliciting preferred-direction saccades are compared for different gaze angles

**FIG. 1.** The monkey uses its eyes (a–c) or head (d–f) to change the initial gaze direction before a saccade. a, d, Each trial begins with a 0.4” diameter fixation point appearing on the tangent screen at eye level. The animal orients its eyes and head toward the stimulus. b, e, The 0.4” stimulus disappears and a smaller, 0.2” diameter stimulus appears at either a different or the same location. The monkey maintains its previous head position and, if necessary, deviates its eyes to fixate the smaller stimulus. c, f, After 1,500 ms the fixation light is turned off and another 0.2” stimulus appears at a peripheral location. The monkey saccades to the new location while keeping its head still, and the sensory and saccade activities are recorded. For cells with both visual and saccade activity, the visual receptive fields and saccadic motor fields overlap one another in oculocentric coordinates and eye position has the same modulation effects on both. Control experiments, using a delayed-saccade task which separates temporally the visual and saccade activities, determined that head position has a similar modulation effect on both visual and saccade activities for individual neurons.

**METHODS.** Experiments were performed in the dark. Gaze direction was recorded using the scleral search coil technique, and head position was recorded using a high-precision potentiometer connected to the head post which allowed the animal to move its head horizontally. Receptive fields were mapped systematically in 8 directions at eccentricities of 8” and/or 16”. If the cell’s receptive field eccentricity was reasonably close to one of these two distances, further tests were made to assess the effects of head and eye position.
in ‘a’, an individual neuron shows highest firing when the visual stimulus calls for eye movement to the SW irrespective of whether the monkeys head, relative to the body, faces left (filled squares) or right (open squares) …yet, firing rates are higher when facing left (contralateral to recorded hemisphere)…’b’ depicts data from the full set of LIP neurons where the preferred direction of each is, for display, centered on x-axis ‘0’

so…the preferred direction of the LIP neurons follows the reference frame of the eye and ‘gain fields’ for peak response are observed for different head orientations – the direction of gain (+ vs. -) is the same for all LIP neurons
comparison of gaze angles achieved by head movements (with eyes straight) or by eye movements (with head straight to body)…in ‘a’/‘b’, activity in response to preferred-direction stimuli changes depending on gaze whether gaze is given by eye or head movements…in ‘c’, a linear regression for data of ‘a’/‘b’ is given…thus, the relevant frame of reference for LIP neurons is position of the stimulus in eye-centered coordinates and gain fields are seen for gaze angle (whether relative to the body or world is not determined).

FIG. 3 Activity of a cell while the monkey is making identical saccades to the left from a fixation point placed at five different gaze positions on the horizontal plane. Gaze directions of ±16°, ±8° and 0° directions were used in approximately two-thirds of the cells showing significant head effects, and ±24°, ±12° and 0° were used for the remainder. All trials are aligned with the onset of the saccade, indicated by the vertical broken lines. a, The animal has its head oriented towards each of the fixation points, with the eyes centred in their orbits before each saccade. b, The head of the animal is directed towards the centre of the screen (0°) with the eyes deviated towards each of the fixation points before each saccade. c, Magnitude of the cell’s activity around the time of the saccade (25 ms before to 75 ms after onset of the saccade) as it varies with initial gaze position. Bars indicate one standard error. A linear relationship of activity with gaze direction was confirmed by a significant linear regression (P = 0.009 for head, P = 0.023 for eye) and by a non-significant analysis of variance (ANOVA) of the regression residuals (P = 0.992 for head, P = 0.944 for eye).
potential topics for term paper (2-page, 1.5-spaced, up to 5% final grade bonus)

- bird caching of food
- ants navigation / dead reckoning
- cross-generation navigation (butterflies)
- Picasso / Pollock / Dalí / Van Gogh tool directions
- homing pigeons and electromagnetic space
- territorial / social space
- the distal reward problem
- temporal discounting
- the man who lost his body
- backwards causation
- crossover of space, time, and language
- prism adaptation
- the pineal gland
- internal alarm clocks
- the Pinocchio effect
- the binding problem
- hemineglect
- Steiner lines
- tool use / extended personal space
- Einstein’s brain
- space in memory and reality
- snapshot consciousness