A Vestibular Sensation: Probabilistic Approaches to Spatial Perception (II)

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Vestibular Responses in Dorsal Visual Stream and Their Role in Heading Perception

• Recent experiments identified a potential neural correlate of heading perception in MSTd of the dorsal visual stream.

• More than half of MSTd neurons are multimodal and are tuned both to optic flow and translational motion in darkness.
  – Previous studies showed that neuronal responses in darkness are driven by vestibular signals.
Vestibular Responses in Dorsal Visual Stream and Their Role in Heading Perception

• Two groups of multimodal MSTd cells
  – “congruent” neurons: similar visual/vestibular preferred directions
    • signal the same motion direction in 3D under both unimodal (visual or vestibular) stimulus conditions
  – “opposite” neurons: prefer nearly opposite directions under visual and vestibular stimulus conditions
Vestibular Responses in Dorsal Visual Stream and Their Role in Heading Perception

- Neural activity in 2AFC heading discrimination task showed that congruent and opposite neurons have different, but complementary, roles in heading perception.
- When the cues were combined (bimodal condition), tuning became steeper for congruent cells but more shallow for opposite cells.
The effect on tuning steepness is reflected in the ability of an ideal observer to use a congruent or opposite neuron’s firing rate to accurately discriminate heading under visual, vestibular, and combined conditions.

For congruent neurons, the neurometric function was steepest in the combined condition – they became more sensitive, i.e., can discriminate smaller variations in heading when both cues are provided.

Opposite neurons are less sensitive during bimodal stimulation.

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• Average neuronal thresholds for bimodal stimulation
  – Congruent MSTd cells: lower than either threshold in the single-cue conditions
  – Opposite cells: higher

• Responses in the vestibular condition were significantly correlated with perceptual decisions
  – Correlations strongest for the most sensitive neurons
  – Only congruent cells were significantly correlated with the monkey’s heading judgments in the bimodal stimulus condition
  – Congruent cells might be monitored selectively by the monkey to achieve near-optimal performance under cue combination
Vestibular Responses in Dorsal Visual Stream and Their Role in Heading Perception

- Recent studies had trained animals perform the heading discrimination task where visual and vestibular cues were put in conflict
  - bimodal neural responses well fit by a weighted linear sum of vestibular and visual unimodal responses
  - weights dependent on visual coherence
  - MSTd neurons appear to give more weight to the strongest cue and less weight to the weakest cue

- In Summary, experiments in MSTd propose two general approaches to the neural basis of vestibular multisensory self-motion perception
  - cortical vestibular responses quantified in the context of a perceptual task performed around psychophysical threshold
  - neuronal visual/vestibular cue integration studied in behaviorally relevant way
Contribution of Vestibular Signals to Body Tilt Perception and Spatial Orientation

• Human and primates orient themselves using gravity
• Spatial orientation: our (change in) orientation relative to gravity (tilt)
• Subjects with defects in their vestibular system have severe spatial orientation
• *Einstein’s equivalence principle*
  – inertial accelerations experienced during self-motion are physically indistinguishable from accelerations due to gravity
• Otolith organs: linear acceleration sensors
  – detect net acceleration
  – cannot distinguish its source
Translation Interpreted as Tilt

- Vestibular system cannot disambiguate tilts relative to gravity and inertial accelerations at low frequencies
- Brain’s default solution is to interpret low-frequency linear accelerations as tilt
- Bayesian framework explains the prevalence of tilt perception by a zero inertial acceleration prior
- At high frequencies, vestibular sensory likelihood function is relatively narrow
  - sensory evidence dominates
- At low frequencies, vestibular sensory likelihood function is relatively broad
  - prior dominates; tilt
Tilt Interpreted as Translation

- Off-vertical axis rotation (OVAR)
Role of Vestibular Signals in the Estimation of Visual Vertical

- **Orientation constancy**: ability to maintain accurate percept of allocentric visual orientation despite changes in head orientation; *earth-vertical*
  - neural representation of the visual scene is modified by static vestibular/approprioceptive signals that indicate the orientation of the head/body
- Static vestibular/somatosensory cues can generate a robust percept of earth-vertical (i.e., which way is up?)
- A-effect: underestimate the true vertical orientation for tilts greater than 70
- E-effect: overestimate the subjective vertical for small angles
Role of Vestibular Signals in the Estimation of Visual Vertical
Role of Vestibular Signals in the Estimation of Visual Vertical

- Bayesian approach in the interpretation of noisy sensory information
  - estimation of the visual vertical biased by *a priori* assumption about the probability of a particular tilt
  - assuming subjective vertical most likely aligned with the long axis of the body
Visual Constancy and Spatial Updating

- Visuopatial constancy: perception of a stable visual world despite constantly changing retinal images caused by eyes, head, and body movements
- A typical spatial updating paradigm for passive movements includes
  - the subject fixates a central head-fixed target
  - a peripheral space-fixed target is briefly flashed
  - the subject is either rotated or translated to a new position (while maintaining fixation on the head-fixed target that moves along with them)
  - the subject makes a saccade to the remembered location of the space-fixed target
- Poor performance suggests inability to integrate stored vestibular signals with retinal information
Visual Constancy and Spatial Updating

- Subjects are able to localize remembered, space-fixed targets better after roll rotations.
- Spatial updating about the roll axis from an upright orientation was ten times more accurate than updating about the roll axis in a supine orientation.
- Roll rotations likely use dynamic gravitational cues, resulting in relatively accurate memory saccades.
- In contrast, subjects partially update the remembered locations of visual targets after yaw rotations.
Visual Constancy and Spatial Updating

• Both humans and trained macaques can compensate for traveled distances in depth and make vergence eye movements that are appropriate for the final position of the subject relative to the target
• Trained animals lose their ability to properly adjust memory vergence angle after destruction of the vestibular labyrinths
• Previous studies also suggest a dominant role of otolith signals for the processing of both self-motion information and spatial updating in depth
• Neural basis of how vestibular information changes the goal of memory-guided eye movements remains to be explored
Concluding Remarks

• Vestibular-related activity is found in multiple regions of the cerebral cortex, where most of these neurons are multisensory
• Characterizing vestibular responses by both their mean values and neuronal variability
• Trying to understand the functional significance of diverse cortical representations of vestibular information; testing vestibular signals in behaviorally relevant task
• From a computational standpoint, it is also important to find out how well the Bayesian framework explains the diversity of behavioral data
  – do our brains really make use of the variability in neuronal firing?
  – how realistic is it that our brains actually implement such a complex framework?