## Self-motion perception: Multisensory integration in extrastriate visual cortex

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Optic flow patterns generated during self-motion provide a strong cue for the perception of our own movement through space (heading). However, accurate judgments of heading often require integration of visual and nonvisual cues, including vestibular, kinesthetic, and eye movement signals. This sensory integration is complicated by the fact that signals from different modalities may originate in different coordinate frames (e.g., eye-centered or head-centered). To investigate the neural basis of self-motion perception, we record from neurons in area MSTd of macaque monkeys during optic flow (*Visual* condition), real motion (*Vestibular* condition) and congruent combinations of the two (*Combined* condition) using a novel virtual reality system that can move animals along arbitrary paths through a 3D virtual environment.

To examine how visual and vestibular signals in MSTd contribute to heading perception, we train animals to perform a fine self-motion discrimination task. Heading directions are varied in small steps around straight forward, and monkeys report whether their heading is to the right or left of straight ahead. Psychophysical thresholds averaged 1-3° and, although the most sensitive MSTd neurons had thresholds close to behavior, the average neuron was much less sensitive than the monkey under both single-cue conditions. In the Combined condition, psychophysical thresholds were significantly lower than in the single-cue conditions and very close to predictions of optimal cue integration theories. According to whether the visual and vestibular heading preferences were well matched or nearly opposite, MSTd neurons could be divided into two distinct groups: 'congruent' and 'opposite' cells. We found that neuronal thresholds in the combined condition were strongly dependent on congruency of heading preferences, such that 'congruent' neurons showed substantially lower thresholds under cue combination, whereas 'opposite' cells showed elevated thresholds. The effect of cue combination on 'congruent' cells was very similar to that seen behaviorally, suggesting that this subset of MSTd neurons may contribute to sensory integration for heading perception.

To assess functional coupling between MSTd responses and perceptual decisions, we compute 'choice probabilities' (CPs), which characterize the trial-to-trial covariation between neural responses and the animal's choices. CPs were strongest under the Vestibular condition, in which ~30% of MSTd neurons showed significant positive effects and the mean CP (0.56) was significantly greater than chance (0.5). In contrast, CPs in the Visual condition depended strongly on the congruency of visual and vestibular heading preferences. 'Congruent' neurons were positively correlated with choices in the Visual condition (mean CP=0.59), whereas 'opposite' neurons tended to be negatively correlated (mean CP=0.45) with heading percepts. These results provide

the first evidence that links cortical vestibular signals with heading perception. In addition, our Visual CP data suggest strongly that the visual responses of MSTd neurons are read out differently depending on the congruency of visual and vestibular tuning preferences. This result supports the notion that 'congruent' cells may have a privileged role in cue combination, and highlights the importance of studying multi-sensory integration for understanding spatial perception.