Distinct Codes As A Substrate For Causal Inference In Primate Superior Colliculus Neurons

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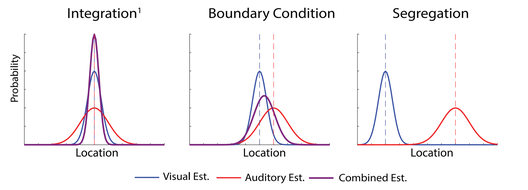
Introduction

Perceptual experience, and its usefulness for guiding behavior in the real world, often depends on the combination of information across multiple senses. Combining information from multiple sensory modalities can make it easier to detect stimuli, perceive location, or understand speech. However, these effects require that only some sensory cues are combined while others are kept separate. This suggests that there are at least two underlying perceptual strategies, one for cue integration and one for cue segregation.

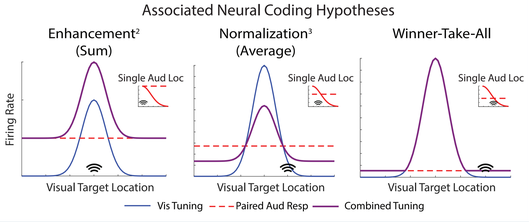
We analyzed single unit activity from a multisensory structure (the superior colliculus, or SC) while monkeys performed an audio-visual localization task requiring both integration and segregation of sensory information. We find that neural combination rules differ greatly between neurons, but that individual neurons do not shift from one rule to another in a way that matches the shift seen in behavior. This suggests that behavioral causal inference may rely on a population level interaction between neurons representing different possibilities (i.e., same or different source for a given stimulus pair).

Multisensory Perception And Related Neural Codes

Perceptual estimates are known to transition between optimal integration and complete segregation (no interaction between stimuli).



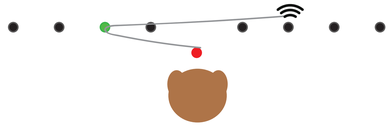
Summation and weighted averaging have both been suggested as neural codes for integrated stimuli, while it is assumed that in the segregated condition a neuron ignores cross-modal information and instead each neuron represents only a single stimulus.



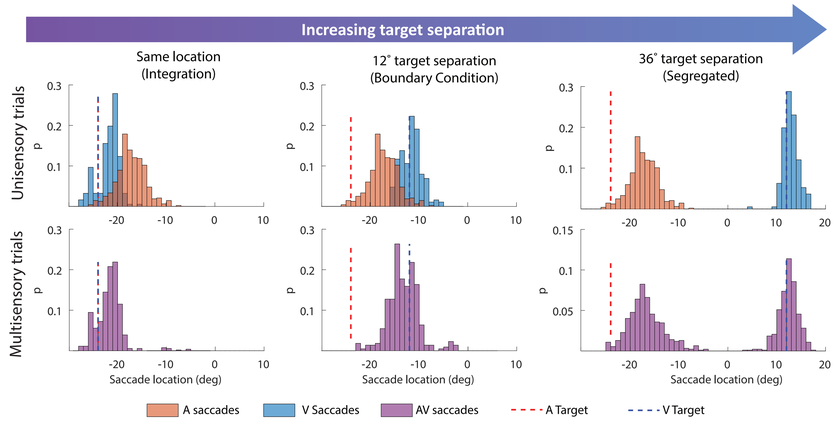
Methods

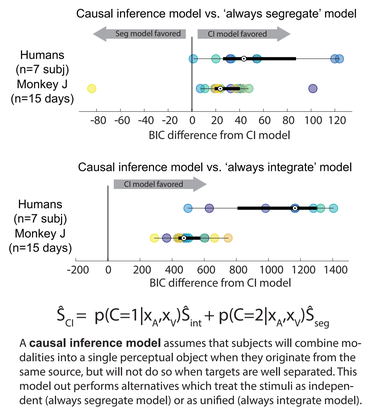
Single unit neural activity is recorded from the superior colliculus while monkeys perform a behavioral task requiring them to localize targets indicated by LEDs or white noise.

Monkeys make saccades to either one or two targets:
- Unimodal targets (auditory or visual, one saccade)
- Unified multi-modal targets (same location, one saccade)
- Separate multi-modal targets (different locations, two saccades)
- Difficult multi-modal targets (close locations, one or two saccades)



Monkey Behavior Shifts From Cue Integration To Segregation As Target Separation Increases



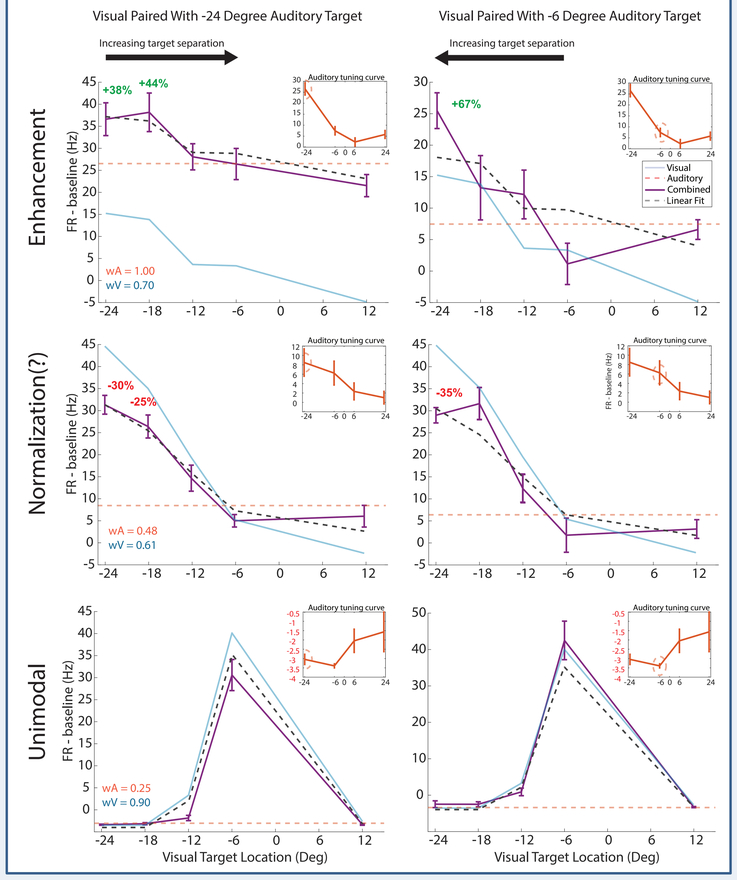


$$\hat{S}_{CI} = p(C=1|x_A,x_V)\hat{S}_{int} + p(C=2|x_A,x_V)\hat{S}_{seg}$$

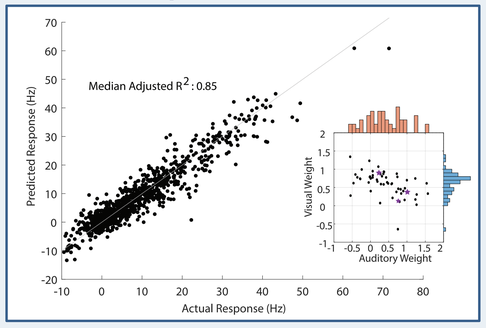
A **causal inference model** assumes that subjects will combine modalities into a single perceptual object when they originate from the same source, but will not do so when targets are well separated. This model out performs alternatives which treat the stimuli as independent (always segregate model) or as unified (always integrate model).

A Diversity of Combination Rules Across Neurons

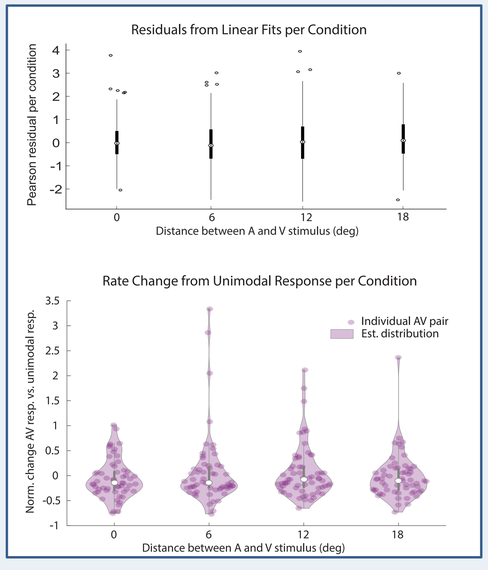
Combined Resp. = wA(Aud Resp.) + wV(Vis Resp.)



One Fit Adequate Across Conditions



Rule Does Not Depend On Separation

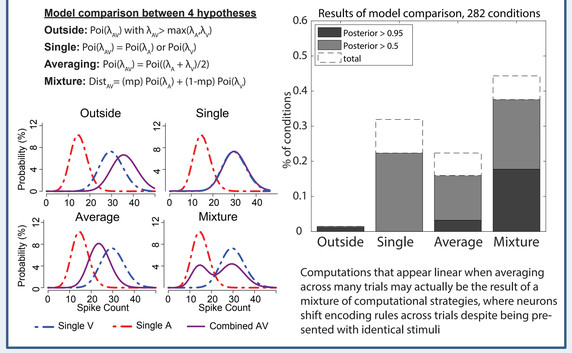


'Average' Response May Be The Result Of A Winner-take-all Mixture Pooled Across Trials

Previous analyses assume that the neuron uses the same combination rule on every trial. Using a Bayesian model comparison allows us to characterize responses on each trial.

Method[4]:
(1) Fit Poisson distributions for single modality (auditory alone or visual alone) trials
(2) Generate predicted distributions under 4 potential combination rules (below)
(3) Compare predictions to actual distributions of single trial spike counts on combined trials
(4) Compute intrinsic Bayes factors between models to determine best model fit for particular condition

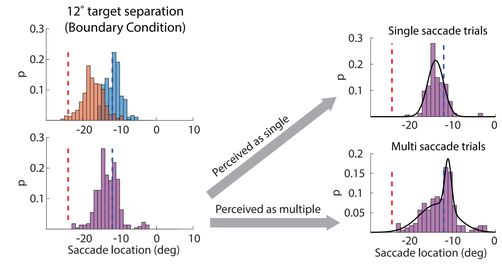
Model comparison between 4 hypotheses
Outside: Poi(λ_{AV}) with $\lambda_{AV} > \max(\lambda_A,\lambda_V)$
Single: Poi(λ_{AV}) = Poi(λ_A) or Poi(λ_V)
Averaging: Poi(λ_{AV}) = Poi(($\lambda_A + \lambda_V$)/2)
Mixture: Dist$_{AV}$= (mp) Poi(λ_A) + (1-mp) Poi(λ_V)



Computations that appear linear when averaging across many trials may actually be the result of a mixture of computational strategies, where neurons shift encoding rules across trials despite being presented with identical stimuli

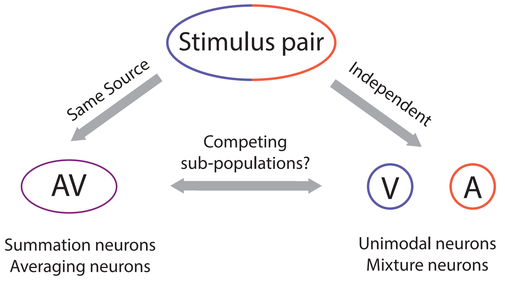
Summary

1) Monkeys performing a multisensory localization task combine information in a manner consistent with causal inference



2) Individual SC neurons are well described by single combination rules during the sensory period rather than switching from enhancement to suppression as target separation increases.

3) This suggests that causal inference seen at the behavioral level may depend on interactions between sub-populations of cells using different encoding strategies, rather than single neuron computations



Acknowledgments
Thank you to V. Caruso, N. Jun, W. Xiao, and S. Willett for input on this work

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Funding
NSF Grant 0924750
This work is supported in part by an NDSEG fellowship