V1 serves as a motor cortex for visually guided saccades: evidence from human and monkey behavioral and neural data

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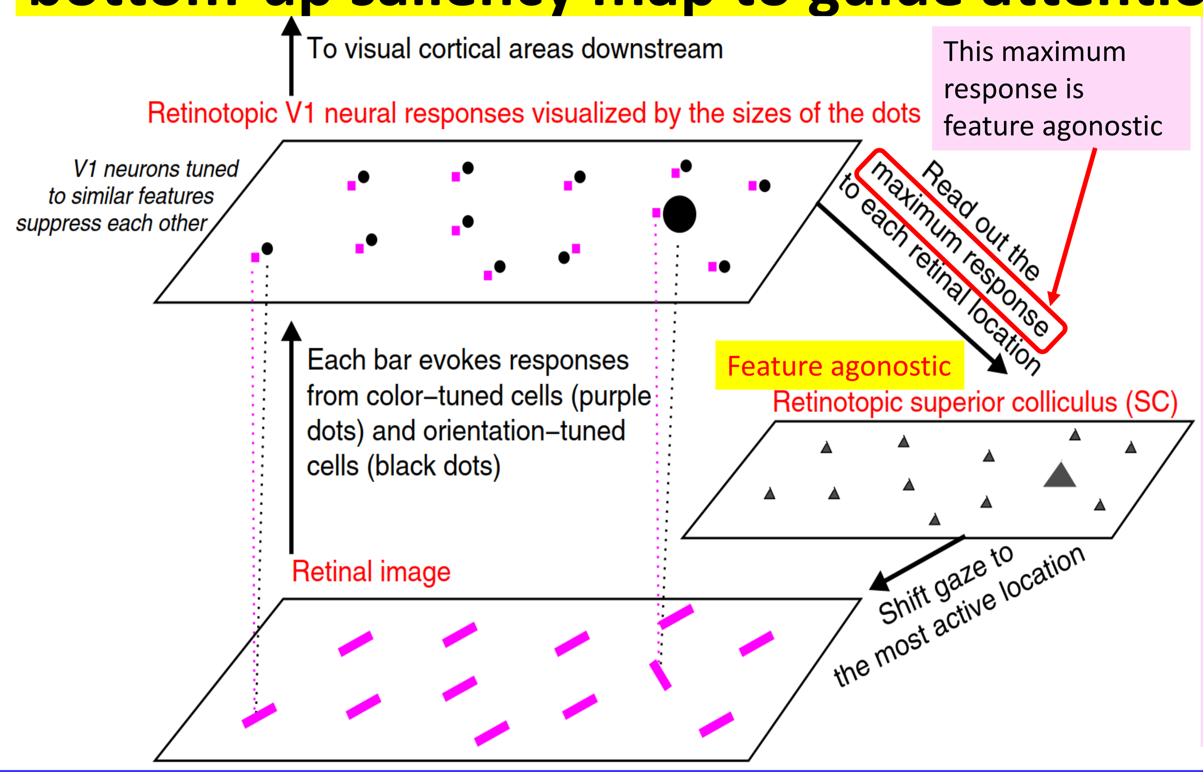
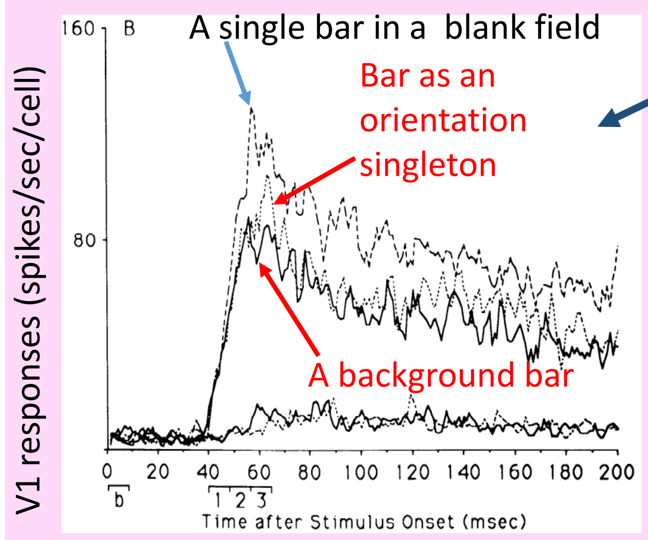
Abstract: I proposed in the late 1990s and early 2000s that the primary visual cortex, V1, creates a bottom-up saliency map from visual inputs (Li 1999, 2002). This is the V1 Saliency Hypothesis (V1SH). According to V1SH, the highest V1 response to any visual location represents this location's saliency, defined as the strength of exogenous attentional attraction. Hence, the visual location evoking the largest V1 response is most likely to attract visual attention or evoke a gaze shift driven by bottom-up visual inputs. For example, a vertical bar in a background of horizontal bars is salient; so is a red dot among green dots, because the feature singletons evoke higher V1 responses than the homogeneous background items. Contextual influences via the intracortical horizontal connections make V1 neurons' responses dependent on contextual inputs outside the classical receptive field (e.g., Knierim & van Essen 1992). These contextual influences are such that neurons tuned to the same or similar features suppress each other, so that the neurons preferring and responding to the homogenous background inputs suppress each other's responses. The neurons responding to the feature singletons escape such suppression and the singletons are thus salient. Here I review some of the supporting evidence in human and monkey data from past works by my collaborators and myself. In lower vertebrates, the saliency map resides in the superior colliculus/optic tectum (Zhaoping 2016). More info. at http://www.lizhaoping.org/zhaoping/V1Saliency.html

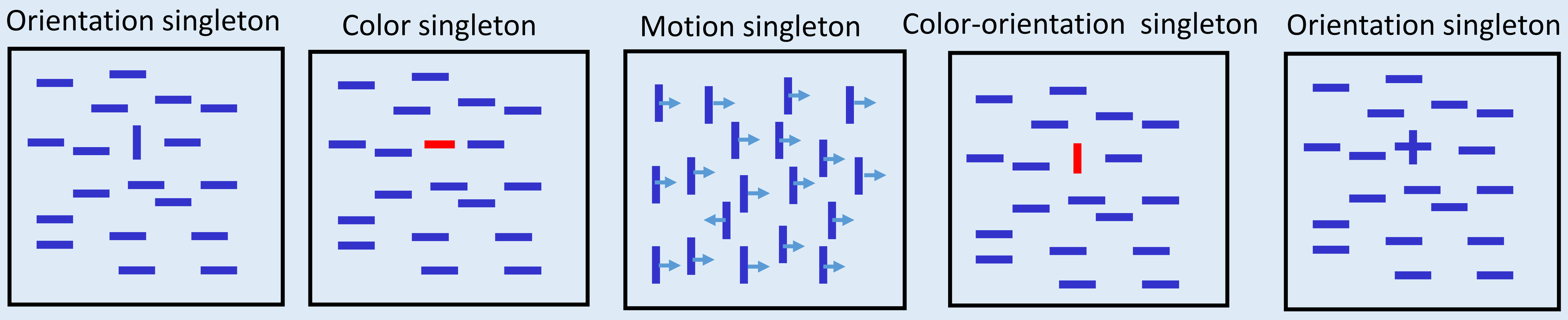
V1 Saliency Hypothesis (V1SH, Li 1999, 2002): V1 creates a bottom-up saliency map to guide attentional/gaze shifts



Fast time course of contextual influences (appear at 40-60 ms after stimulus onset) in V1 (Knierim & vanEssen 1992)



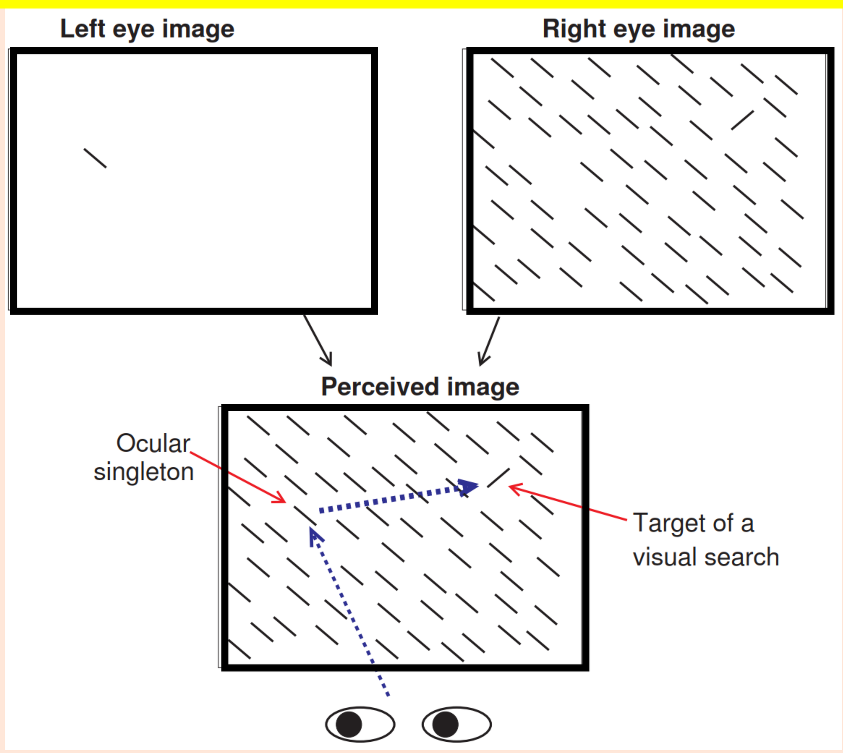
V1SH explains why color, orientation, and motion feature singletons attract attention



- Orientation singleton: Neuron responding to the vertical bar escapes iso-orientation suppression
- Color singleton: Neuron responding to the red bar escapes iso-color suppression
- Motion singleton: Neuron responding to the left-ward moving bar escapes iso-motion-direction suppression
- Color-orientation singleton: Neurons responding to the red-vertical bar escapes iso-orientation and/or iso-color suppression
- Orientation singleton: No need to have a V1 cell tuned to the cross for the cross to attract attention, since the neuron responding to the vertical bar escapes iso-orientation suppression.

V1 neurons are tuned to orientation, color, or motion direction, and some of them tuned simultaneously to color and orientation, or to motion direction and orientation

V1SH prediction: Attention capture by an eye-of-origin singleton --- because V1 neurons are tuned to eye-of-origin, and V1 has iso-eye-of-origin suppression --- confirmed experimentally (Zhaoping 2008, 2012)

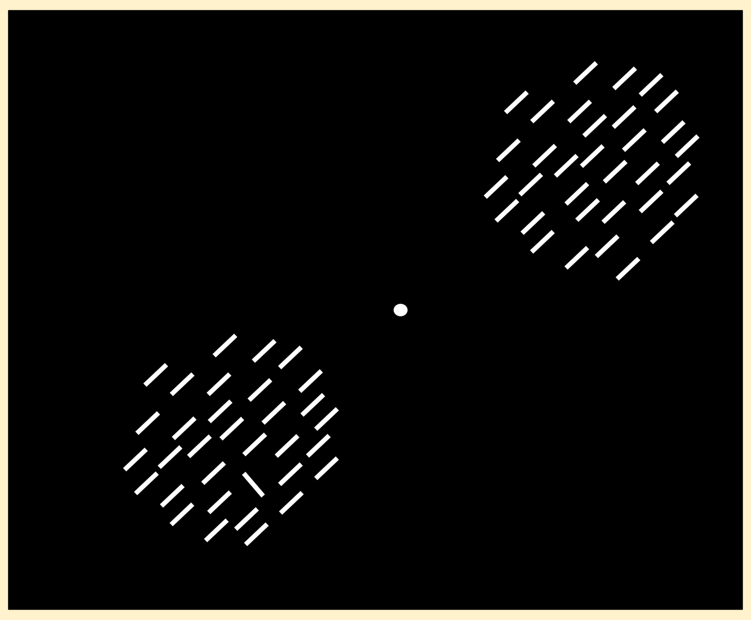


An ocular singleton, though irrelevant in a task to search for an uniquely oriented bar, pops out to attract attention and gaze shift, even though observers do not find it visually distinctive and are often unaware of its presence. This attraction prolongs reaction time (RT) to find the target. This observation (Zhaoping 2008, 2012), predicted by V1SH, is a fingerprint of V1, which is the only cortical area with a substantial number of neurons tuned to eye-of-origin of visual inputs.

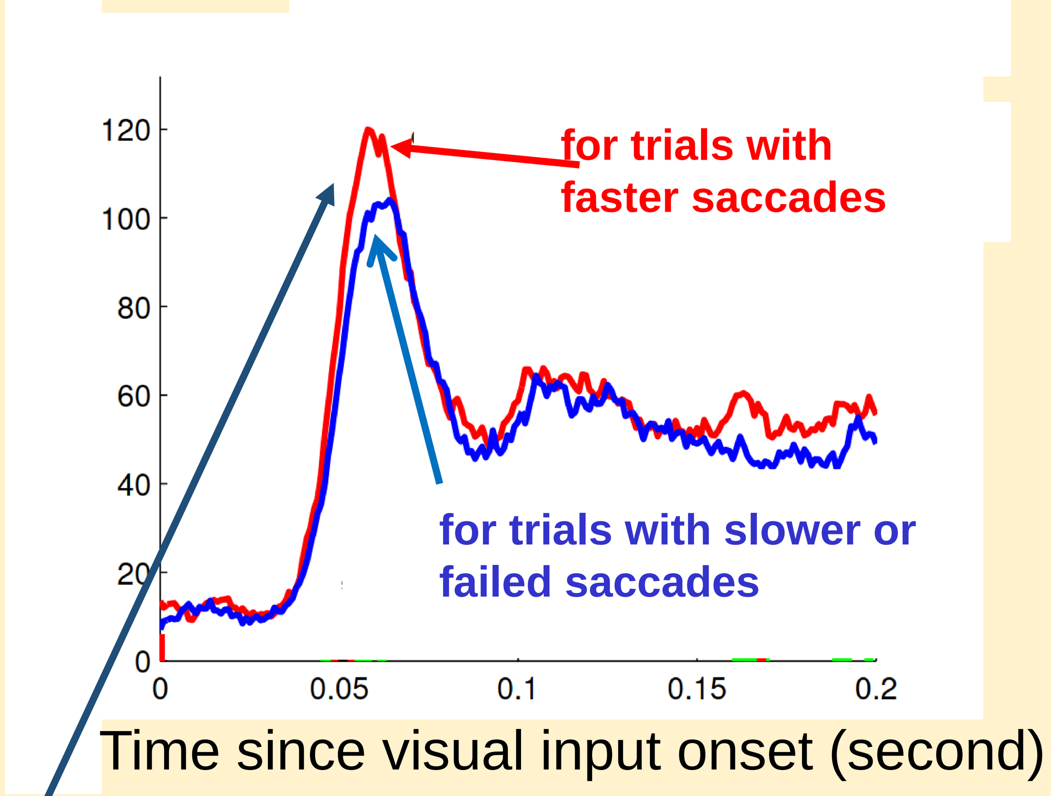
In the dichoptic input above, the uniquely oriented bar is salient, because the V1 neuron tuned to and responding to it escapes iso-orientation suppression. The ocular (eye-of-origin) singleton is also salient, because the responding neuron escapes the iso-eye-of-origin suppression. In this example, the ocular singleton is task irrelevant but is more salient than the orientation singleton, attracting the first saccade in the search task.

V1SH prediction: given the same visual input, higher V1 responses (due to neural response fluctuations or optogenetic stimulation) should lead to faster saccades to the feature singleton --- confirmed experimentally in monkeys (Yan et al. 2018)

Monkey's task: start a trial by fixating at the central fixation point; after the bars appear, saccade to the orientation singleton (whose position is unpredictable) as quickly as possible



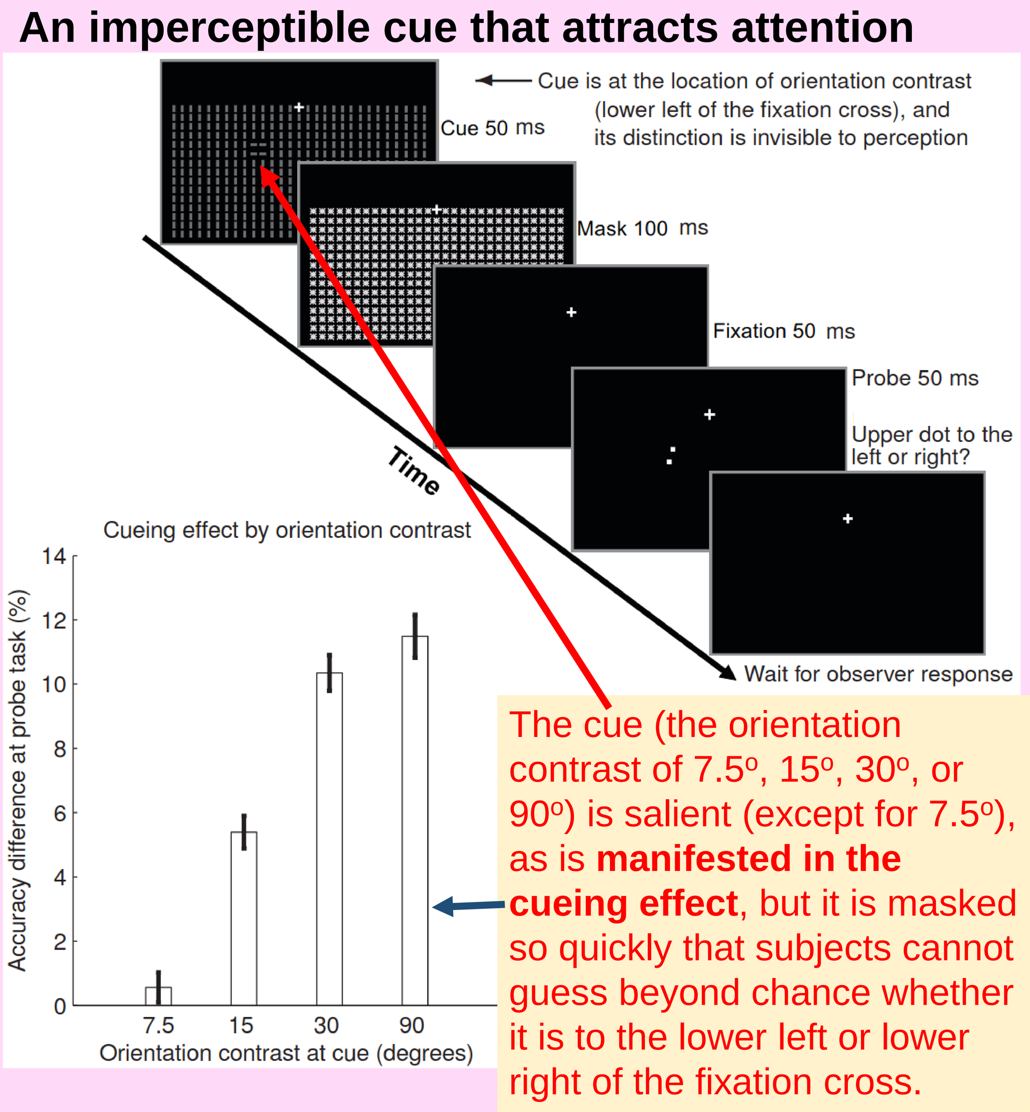
V1 neural responses to the orientation singleton (spikes/sec) before the saccade onset (usually > 200 ms)



V1 neurons' responses to the search target were measured while the monkey was doing the task. Usually it took more than 200 ms after stimulus onset before the saccadic onset. **At around 40-50 ms after the stimulus onset, given the same visual inputs, trials with higher initial V1 neural responses to the target were more likely to evoke faster and accurate subsequent saccades to the target**. This latency, at 40-60 ms, is so short that higher cortical areas or superior colliculus could not have provided this saliency signal to V1. This latency agrees with the time course of **the contextual influences** observed in Knierim and van Essen 1992. White et al. 2017 did not see this saliency signal at this short latency, but they saw a signal at a latency longer than that in superior colliculus, in their monkeys doing a similar task. Yan et al. 2018 showed that a signal at such a longer latency arises from top-down factors.

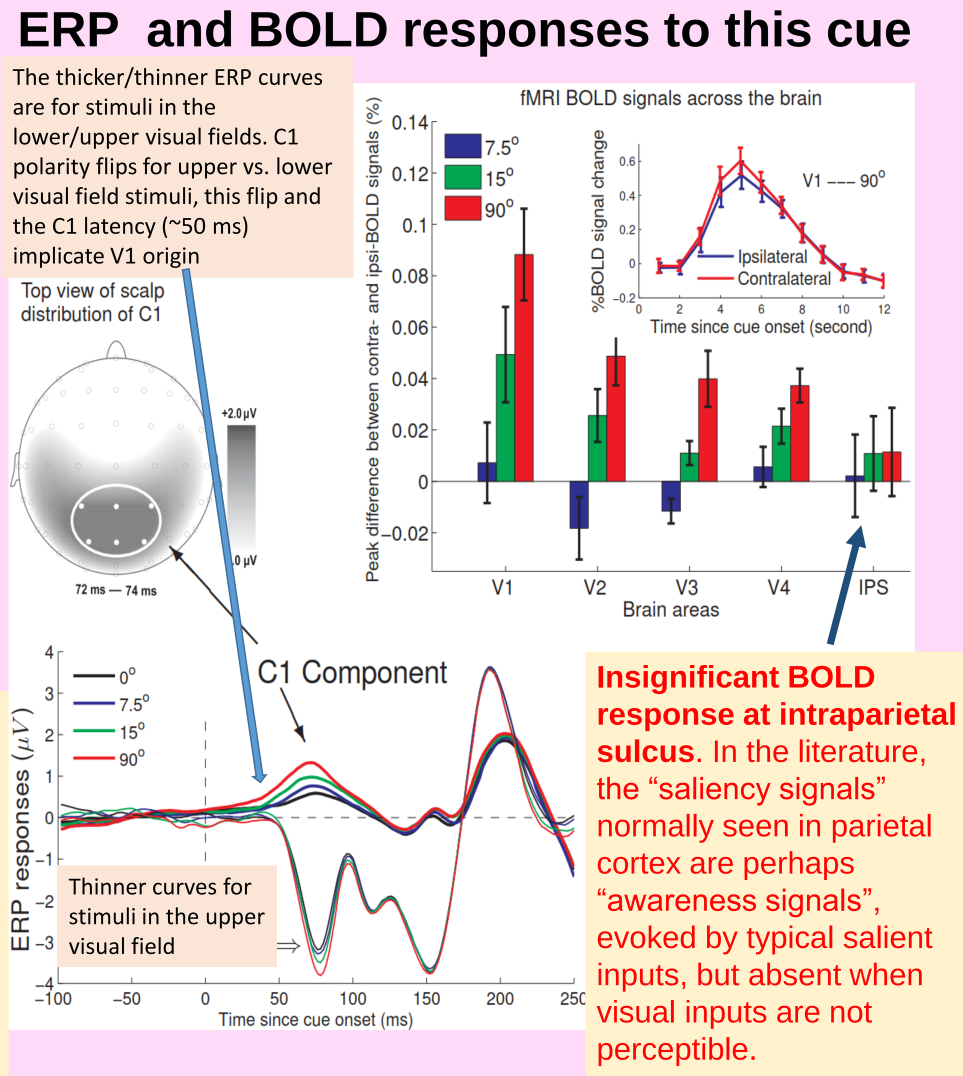
fMRI/ERP evidence: salient but imperceptible inputs (the cue below) activate early visual cortex but not the parietal cortex (Zhang, Zhaoping, Zhou, Fang, 2012)

An imperceptible cue that attracts attention



The cue (the orientation contrast of 7.5°, 15°, 30°, or 90°) is salient (except for 7.5°), as is **manifested in the cueing effect**, but it is masked so quickly that subjects cannot guess beyond chance whether it is to the lower left or lower right of the fixation cross.

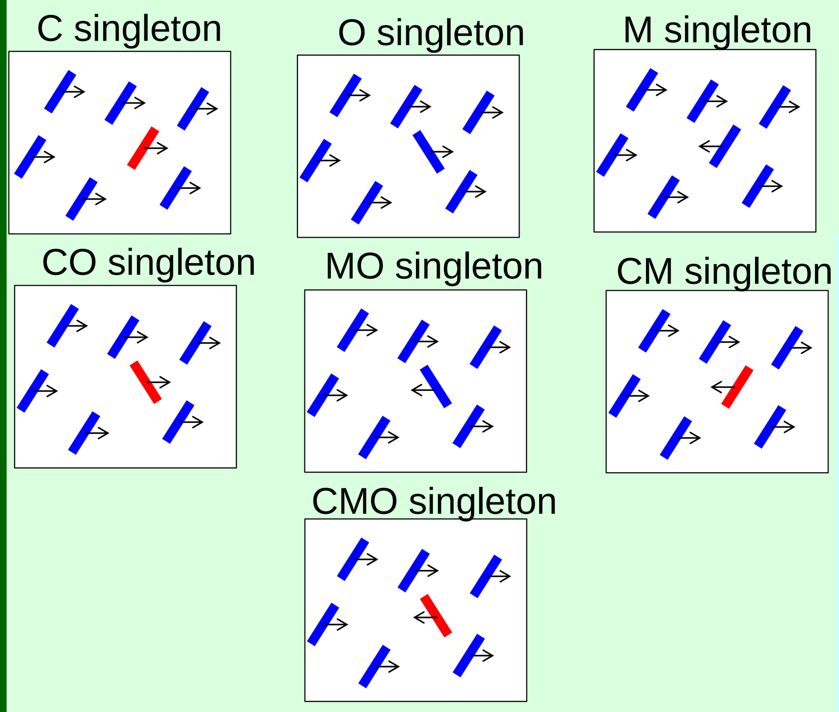
ERP and BOLD responses to this cue



Insignificant BOLD response at intraparietal sulcus. In the literature, the "saliency signals" normally seen in parietal cortex are perhaps "awareness signals", evoked by typical salient inputs, but absent when visual inputs are not perceptible.

V1SH fully predicts reaction times using zero parameters, suggesting that V2 and other visual cortical areas do not contributing to saliency computation

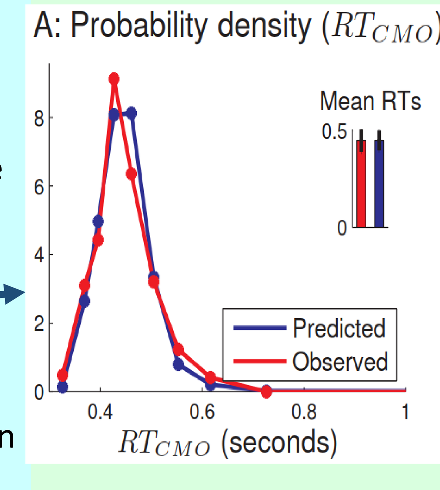
(Koene & Zhaoping 2007, Zhaoping & Zhe 2015)



Mathematically, V1SH predicts the RT, RT_{CMO}, of detecting singleton pop out by triple-feature (CMO) uniqueness in color (C), motion direction (M) and orientation (O) from RTs for single- and double-feature uniqueness (RT_C, RT_M, RT_O, RT_{CM}, RT_{MO}, RT_{CO}) by equation

$$\min(RT_{CMO}, RT_C, RT_M, RT_O) = \min(RT_{CM}, RT_{CO}, RT_{MO})$$

This prediction uses no parameters, and is derived from the fact that V1 has no cells simultaneously tuned to color, orientation, and motion direction. V2 and other extrastriate cortical areas do have such cells, so if they were involved in the saliency computation, the equality above would become an inequality. **RT data is consistent with the V1 prediction, suggesting that V2 and above do not contribute to the saliency computation** (though they could contribute to guide attention by top-down endogenous control).



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