Divisive normalization as a mechanism for hierarchical causal inference in motion perception

Causal inference (CI) has been proposed as a universal computational motif in the brain [Shams & Beierholm 2020]. However, its neural implementation is unclear. Likewise, Divisive Normalization (DN) has been proposed as a canonical circuit motif [Heeger 2011], but there are competing theories about the computations that DN implements (gain control, attention). In this work, we unified both by showing how an extended DN model can account for neural predictions made by a CI model [Shivkumar et al. 2022] in the context of hierarchical motion perception.
Specifically, we generated CI predictions for neural responses to a center-surround stimulus. CI makes interesting predictions for neural responses encoding two latent variables in the model: retinal and relative velocities. These predictions (supported by preliminary data) resemble the responses of two previously described classes of neurons in area MT: those with antagonistic or integrative surround [Born & Bradley 2005]. We investigated whether DN could be a potential mechanism that implements CI computations by fitting it to the CI predictions. Classic DN postulates that each neuron's response is divisively modulated by pooling the activity of neighboring neurons. We analytically showed that a normalization pool that only incorporates the activities of neurons responding to center and surround stimuli alone cannot explain the complex CI responses. Instead, we found that a normalization pool that additionally includes multiplicative interactions between the center and surround activities can explain our CI predictions. We used tuning properties of MT neurons [DeAngelis & Uka 2003] to generate both: (a) biologically-realistic CI predictions and (b) a realistic normalization pool. We showed that the same DN model can explain CI neural predictions across different center-surround speeds. Our results suggest that an extended DN architecture, with interaction terms in the normalization pool, may serve as a mechanism to implement CI at the neural circuit level.

Causal inference (CI) predicts complex center-surround interactions for neural responses

Our percept of object velocity has been found to be affected by the velocities of other objects in the scene. This has been previously modeled as arising from CI computations with empirical support from human psychophysics [Shivkumar et al. 2022]. In their task, observers' percept of the center velocity (green dots) in a classic center-surround stimulus (Fig. 1A) was biased: (a) towards the surround velocity when the center and surround were inferred to move together, and (b) towards the relative velocity (blue arrow in Fig. 1A) otherwise. The key motif in their model (Fig. 1B) inferred the retinal velocity of the center stimulus as the sum of the surround velocity and the relative velocity between the center and the surround. The mixture prior over the relative velocity "chunked" similarly moving objects. We show the neural predictions for a neuron encoding the relative velocity (Fig. 2A) for different center-surround speed combinations (different panels) and different center-surround direction combinations (axes) by generating posterior samples from the model and passing them through the measured tuning curve of the neuron (method validated in [Shivkumar et al. 2022]). We use previously measured tuning curves from alert macaque monkeys [DeAngelis & Uka 2003] to generate the CI neural predictions in Fig. 2A. CI predicts interesting non-separable interactions between center and surround velocities for neurons encoding the relative velocity variable. The predicted response is high when the inferred relative velocity is close to the neuron's preferred velocity (0 deg. preferred direction and 7 deg/s preferred speed). For comparable speeds (first and fourth panel), center and surround velocities together determine the response pattern. The peak occurs when the *relative velocity* (computed by mapping each point in the 2D surface to velocity vectors and taking their difference) is aligned with the neuron's preferred velocity. However, for large speed differences, the larger velocity dominates the relative velocity resulting in center-dominated (peak of activity around 0 deg. center direction, i.e. neuron's preferred direction in the third column) or surround-dominated tuning curves (peak of activity around $\pm$ 180 deg. surround direction in the second column).

An extension of the classic DN model explains the responses predicted by CI

At the neural circuit level, the mechanisms by which CI computations are implemented remain elusive (also see [Coen-Cagli et al. 2015]). To explain the neural predictions from the CI model, we expanded the normalization pool of the classic DN model to incorporate: interaction terms between center and surround neurons, the activities of center neurons (green in Fig. 1C), and the responses of surround neurons (red in Fig. 1C). The addition of the interaction terms allowed the model to account for non-separable variations in the structure of the neural responses shown in Fig. 2A. We use a realistic normalization pool using the tuning properties of 475 MT neurons [DeAngelis & Uka 2003], resulting in a network with 226576 parameters (475 w^c's+ 475 w^s's + 475 $\times$ 475 w^{cs}'s + α). As observed in Fig. 2B, fitting the weights of the classic DN model to match the CI predictions fail to account for the data (R^2 ranging from 1% to 66%). This result occurs because the individual terms for the center and surround neurons can only account for horizontal or vertical stripes in the 2D response profile. On the other hand, fitting our extended DN model (Fig. 2C) better accounts (R^2 between 87% and 98%) for the diagonal structures in the responses by incorporating the center-surround interaction terms. Importantly, the responses in Fig. 2C are generated using the same fitted weight parameters across all speed combinations, i.e., we do not fit different weights to each speed combination. In summary, our results suggest that an extended DN model may serve as a mechanism used by the brain to implement CI computations.

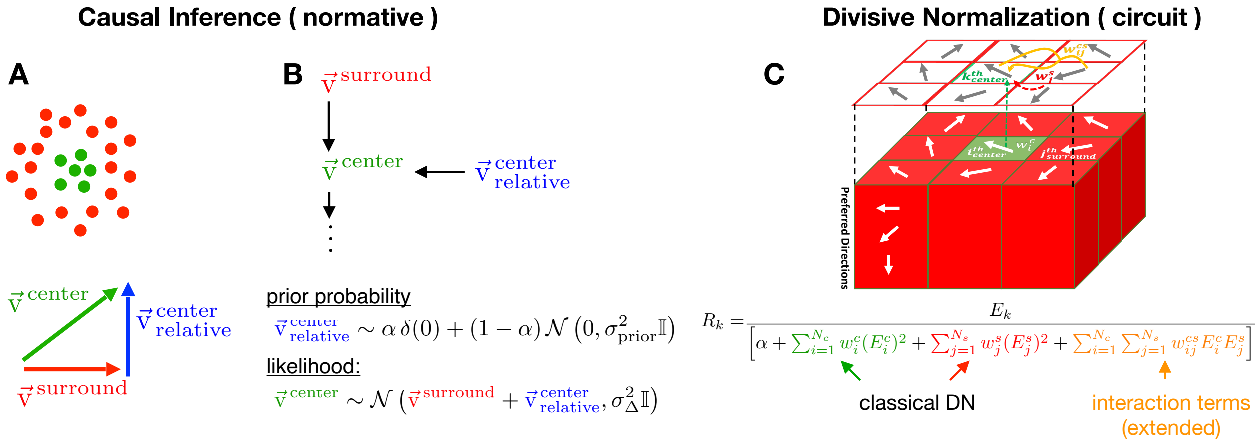

Figure 1. **A:** Stimulus with a moving object (green dots) along with a surrounding group (red dots); corresponding velocities indicated below. **B:** Generative model motif describing how the brain infers whether the object moves with the group or moves relative to it. **C:** Schematic of the extended normalization model with the corresponding equation below.

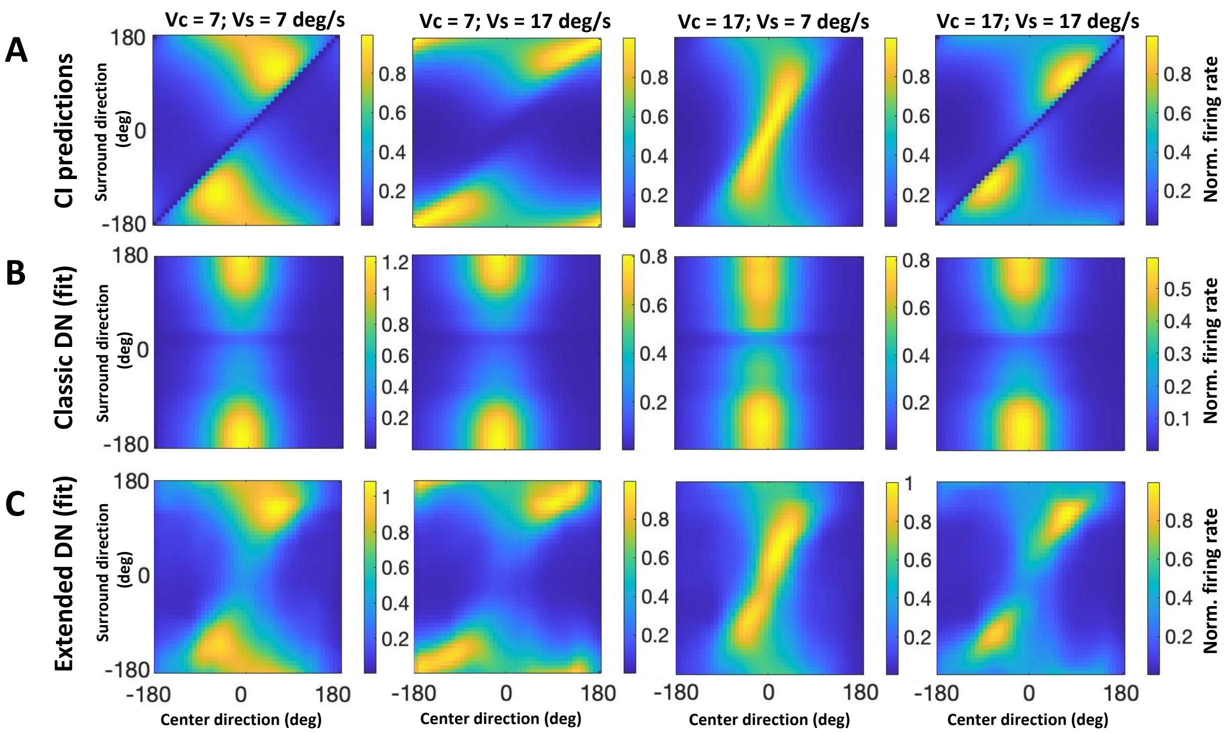

Figure 2. **A:** CI predictions for a neuron evaluated at different center and surround speed combinations. Each panel corresponds to a center (Vc) and surround (Vs) speed combination. **B:** Response of the classical DN model. **C:** Response of our extended DN model.