

Fields of Gain in the Brain

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For more than two decades, neuroscientists have debated the role of “gain fields” in sensorimotor transformations. In this issue of *Neuron*, Chang et al. demonstrate a tight correlation between eye and hand position gain fields in the “parietal reach region,” strongly suggesting that they play a functional role in computing the reach command.

The sensorimotor transformations for goal-directed movements have been studied intensely by neuroscientists, but we still have much to learn about the underlying computational principles used by the brain. In this issue of *Neuron*, Chang et al. (2009) have brought us one step closer to understanding how the brain computes reach plans from visual and postural (i.e., eye orientation, and hand position) signals.

Chang et al. (2009) recorded from neurons in the posterior parietal cortex of monkeys, specifically in an area extending along the medial bank of the intraparietal sulcus toward the parietal-occipital junction. This area has been called the parietal reach region (PRR), because PRR units are spatially selective for visual stimuli when they are used as the goal for reach movements, in contrast to their neighbors along the lateral bank of the intraparietal sulcus (LIP) that are preferentially selective for saccades (Andersen and Buneo, 2002; Snyder, 2000).

In this new study, Chang et al. (2009) reinforce the role of PRR in visuomotor processing for reach, confirming that units in PRR are spatially selective for reach targets, with mountain-like “Gaussian” visual receptive fields whose peaks tend to be fixed relative to current gaze direction. PRR was already thought to show postural modulations (e.g., Andersen and Buneo, 2002), but here, Chang et al. (2009) probe these relationships with greater quantitative detail than previous studies have attempted. First, they show that the receptive fields of PRR neurons are modulated by both initial gaze position and initial hand posi-

tion, in a manner known as a “gain field.” Second, and more importantly, they show that these eye and hand gain fields are not independent or random, but instead have a quite striking interrelationship: the eye and hand gain fields for any given PRR neuron are yoked in such a way that they have equal and opposite strength. Based on these findings, Chang et al. (2009) propose that gain fields are involved in the comparison of eye, hand, and target positions required to compute the desired hand displacement for a reach.

To understand gain fields and the broader significance of these findings, it is necessary to briefly review the relevant physiology and theory from an historical perspective.

Gain fields were first characterized by Andersen and Mountcastle (1983) in neurons located within LIP and visual area 7A. When they tested the visual receptive field for a given neuron at different eye positions, the neuron's action potential frequency increased or decreased as if it were being multiplied by gaze angle, scaled by some constant. Eye position did not change the shape of the visual receptive field, nor its location (relative to the eye in this case): it simply scaled the receptive field up and down by some gain factor, hence: “gain field” (Figure 1A).

Zipser and Andersen (1988) were the first to directly implicate gain fields in the process of visual-motor transformations. They trained artificial neural networks to transform visual target position in an eye-fixed reference frame (i.e., relative to gaze) and gaze position signals into

a signal representing the position of the target location in a space-fixed frame of reference (i.e., relative to coordinate axes that are fixed in space, independent of gaze position). As these authors predicted, the network model spontaneously developed visual receptive fields that were gain modulated by eye position in a nearly identical way to what had been observed in parietal cortex. The logical implication is that eye position gain fields in the brain might perform the same function; they could be the brain's computational means for performing transformations between different reference frames. This formed a beautiful complementary pairing—one of the most influential in systems neuroscience—between theory and experiment.

How do gain fields work? Figure 1A provides a cartoon version of the basic principle behind the Zipser and Andersen (1988) model. In general terms, gain fields (in theory) work at the population level by separately modulating the baseline responses of individual neurons, up- or downregulating their entire receptive field strength. In this way, the brain can alter the relative contributions of each neuron to the overall population output, i.e., the next level in the brain that reads out the population activity. The brain might then integrate the total output of a neural population in many different ways, thus allowing pattern changes related to gain fields to produce very different responses downstream (e.g., a movement plan relative to the eyes, the head, or the hand). For example, in one classic view of visuomotor control, something like the output of the Zipser and Andersen model could

be compared with knowledge of current hand position to compute the desired displacement of the hand toward the target (Figure 1B).

Since their original discovery, eye position gain field modulations of visual signals have been observed in nearly every part of the brain involved in the visual-motor transformations for eye and arm movements, from primary visual cortex to motor cortex and the superior colliculus (Andersen and Buneo, 2002; Boussaoud and Bremner, 1999; Sahani and Dayan, 2003). Other types of signals also produce gain fields, including head position, vergence, target distance, chromatic contrast, and the statistical reliability of the sensory signals themselves, leading to suggestions that gain fields are a general computational mechanism for sensory and sensorimotor processing (Ferraina et al., 2009; Hwang and Shadmehr, 2005; Pouget et al., 2003; Salinas and Sejnowski, 2001; Salinas and Thier, 2000; Solomon and Lennie, 2005).

There are, however, a number of factors that have led some investigators to question the theoretical role that has been attributed to gain fields. First and foremost, even though gain fields are generally accepted as a real neurophysiological phenomenon, they could still be an epiphenomenon arising from the use of eye position signals for some other unknown function and might have nothing to do with the sensorimotor functions that have been theorized to date. Second, gain fields may not reliably influence behavior because other factors, such as noise and attention, also modulate action potential rate. These factors might interfere with each other to negate the

usefulness of gain fields in any purposeful transformation, although contrary theoretical arguments can be made (e.g., Pouget et al., 2003). A potential critique

of the original Zipser and Andersen (1988) model is that very few neurons directly involved in the visual-motor transformation have been shown to resemble the output of their model. Finally, it might be argued that changes in gaze position and/or hand position can be described as a series of displacements, without the need to refer back to eye or hand position.

We have recently shown that the latter critiques related to geometry—the absence of high-level spatial coding and the redundancy of postural commands—break down when one considers the real three-dimensional (3D) geometry of the system, i.e., the way light falls on the retina, the 3D geometry of eye, head, and arm movements, and how they all link together. Here intuition tends to fail, and it turns out that postural signals are mathematically necessary to generate accurate movement commands from visual signals, except for a small range of movements in the central frontal plane. And once again, when network models are trained to perform these transformations, they produce gain-field-like modulations on receptive fields, likewise suggesting that gain fields could be the mechanism that performs the 3D transformations required for gaze and reach movements (Blohm et al., 2009; Smith and Crawford, 2005).

However, the more fundamental critique—that all of this is based on correlations that could be coincidence—is harder to argue away. Moreover, neurophysiologists are notoriously suspicious of pure theory; they

like to see the truth with their own eyes “at the tip of their electrodes.”

Into this mix step Chang et al. (2009) with their current article. In addition to

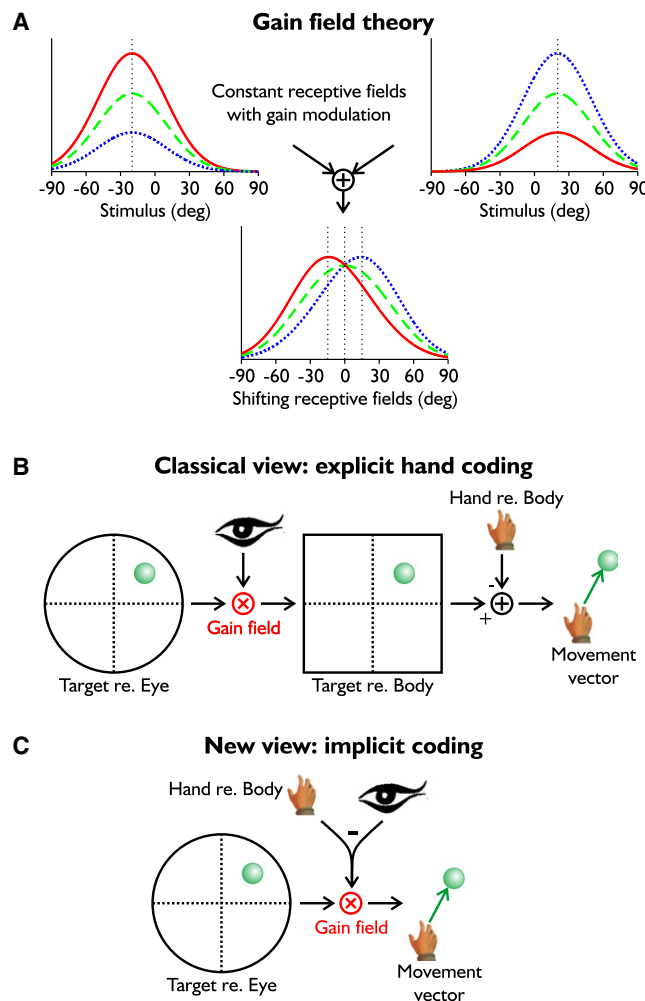


Figure 1. Gain Field Mechanisms

(A) Working principle of gain fields, based on Zipser and Andersen (1988). The upper part of the panel shows the hypothetical receptive fields of two neurons that are gain modulated (e.g., by eye or hand position) in opposite ways without shifting. For example, the three lines in each graph could represent visual receptive fields mapped relative to gaze at a leftward eye position (red solid line), a central eye position (green dashed line), and a rightward eye position (blue dotted line). Here, eye position modulates the strength of response of two neurons, but does not cause them to shift. However, summation of these two gain-modulated neural responses results in shifting receptive fields in the output, e.g., eye position (or in other cases hand position) has shifted the receptive field.

(B) Classical view of motor planning. In this schematic, gain fields are used to transform desired target position from eye coordinates (re: eye) into body coordinates (re: body). Hand position could be explicitly subtracted (–) from the latter to produce the desired movement vector.

(C) A new perspective on movement planning: Chang et al. (2009) advocate that the movement vector could be generated directly if the eye-centered visual receptive fields of the target are gain modulated by both eye and hand positions. The read-out of this implicit computation can then produce the movement vector, providing that eye and hand gain fields have the same strength but opposite sign (–).

providing the data described above, they use the tried-and-true method of training a neural network to perform a transformation. In this case, they trained a model transformation from eye position, target position, and hand position into a hand motor command and found that their model develops the same tight (opposite) relationship between eye position and hand position gain fields observed in their PRR data, logically implicating PRR in this same computation.

One reason why this particular study is superior is because the data and model are independent, but the real strength is in the correlation between eye and hand gain fields. This is so strong that when they replace these separate terms with a single eye-hand distance gain field (representing a vector explicitly used for the calculations in their model), the variance in the data is explained nearly as well: better, if one accounts for the statistical power of a simpler model.

How can this correlation be interpreted? Again, Chang et al. argue that this tight correlation supports a functional role of gain fields and PRR in the computation of the reach plan. In contrast to the classic model illustrated in Figure 1B, in which implicit and/or explicit comparisons with eye and hand position are performed in sequential steps, the data of Chang et al. (2009) suggest a view in which eye and hand gain fields could perform these comparisons implicitly in one step (Figure 1C). This requires eye and hand gain fields have equal strength but opposite signs, exactly as Chang et al. report. Thus, eye-hand gain fields might combine reference frame transformations and movement planning at the same stage.

This is not the end of the gain field debate. It would seem exceedingly unlikely that the relationships described

by Chang et al. (2009) would arise from pure chance, but they are still correlative observations. To causally prove the role of gain fields in sensorimotor transformations one would have to remove them, without affecting other factors, and show that this degrades sensorimotor performance in the expected fashion. This is theoretically possible, but technically very difficult since it would require cutting off the source of these signals without affecting the local circuitry or copies of this signal used for other functions.

Second, it is clear that PRR is just one of many areas involved in the reach transformation. To fully understand the role of gain fields in this process, one must consider the entire cortical and subcortical circuitry for reach, which is both complex and extensive.

Finally, Chang et al. (2009) used standard head-movement restraints and all of their behavioral analysis was based on data obtained from a 2D plane, i.e., the intersection points of gaze and hand position with their visual display/touch screen. This setup likely captures linear effects but not the nonlinear geometry of retinal projection and its dependence on 3D eye and head orientation (Blohm et al., 2009; Smith and Crawford, 2005). These factors become important in real-world circumstances where—as Chang et al. (2009) acknowledge—larger ranges of gaze, target, and hand position may occur.

Further, reach itself is 3D; involving hand displacements in both direction and depth (Andersen and Buneo, 2002; Ferraina et al., 2009; Snyder, 2000), produced by underlying rotations of the upper arm about the shoulder joint, the lower arm about the elbow joint, and the hand about the wrist. None of these factors were measured in the current study, so the role of PRR in these transfor-

mations cannot be explored or excluded on the basis of these data.

Regardless of these limitations, the work of Chang et al. (2009) provides an important step in understanding the physiology of PRR, provides exciting new insight into the potential computational principles of sensorimotor transformations in the brain, and should in time gain its proper place in the historical development of the gain field story.

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