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REVIEW ARTICLE

# Corollary Discharge and Oculomotor Proprioception: Two Mechanisms for Spatially Accurate Perception and Action

*Vincent Sanchez[1,3], Wangzikang Zhang[1,3], Linus D. Sun[1,2,3] and Michael E. Goldberg[1,2,3,4*]*

**Abstract** | Our eyes are in constant motion, therefore, so we cannot solely use retinal information to determine the location of objects in space. Our ability to maintain a stable representation of the world despite a constantly moving eye is a phenomenon that has yet to be fully explained. However, two different mechanisms have been proposed as possible solutions. First, a corollary discharge of the eyes' motor command as the eyes move about, was proposed by Herman von Helmholtz. On the other hand, a spatial representation via proprioceptive signals from nerve endings of eye muscles was proposed by Sir Charles Sherrington. We hypothesize that both mechanisms are used by the brain to achieve spatial accuracy and we present experimental results that support both ideas. While corollary discharge remaps the spatial representation even before an impeding saccade, oculomotor proprioception establishes an accurate spatial representation well after the saccade.

**Keywords:** *Corollary discharge, Proprioception, Receptive field, Remapping, Lateral intraparietal cortex (LIP), Frontal eye field (FEF), Somatosensory cortex*

## 1 Introduction

The only way visual information can enter the brain is through the retina. Our eyes are constantly in motion, so the location of an object on the retina cannot always be useful to determine where an object is in space. The parietal lobe is the region of the cerebral cortex that determines the spatial location of targets for action[1]. Neurons in the parietal cortex ordinarily respond to stimuli in a particular area of the retina, called the receptive field, and the brain must compensate for eye movements to create a spatially accurate representation. In the 19th century, Herman von Helmholtz on one hand, and Wilhelm Wundt and Sir Charles Sherrington on the other, each postulated a different mechanism by which the brain can solve the problem of spatial accuracy. This review will focus on these two mechanisms.

Helmholtz noticed that a diabetic patient with a paralysis of the lateral rectus muscle (the muscle that moves the eye towards the ear) perceived the world to jump towards the nose when he tried to move the paralyzed eye towards his ear[2]. Helmholtz theorized that the brain feeds back a copy of the motor command that would move the eye to the visual system, and that this would compensate for the eye movement. He defined this signal as "the effort of will". He argued that he patient intended to move his eye in one direction, and the brain expected the retinal location of the world to shift in the opposite direction. To stabilize the visual world, the brain fed back the motor signal, thereby canceling the expected retinal shift. Due to paralysis, the eye was unable to move but perceived that the world did, because the motor feedback signal was unopposed. More recently, Helmholtz's 'effort of will' has been called 'corollary discharge' or 'efference copy.' Contrary to Helmholtz, Wilhelm Wundt hypothesized in the 19th century that a measure of the eye position in the orbit could be used to calculate location relative to the head (craniotopic representation)

*Vincent Sanchez and Wangzikang Zhang have contributed equally to this work.*

*[1] Mahoney-Keck Center for Brain and Behavior Research, Department of Neuroscience, Columbia University College of Physicians and Surgeons, New York, NY 10032, USA. [2] Departments of Neurology, and Ophthalmology, Columbia University College of Physicians and Surgeons, New York, NY 10032, USA. [3] Division of Neurobiology and Behavior, New York State Psychiatric Institute, New York, NY 10032, USA. [4] Departments of Neurology, Psychiatry, Columbia University College of Physicians and Surgeons, New York, NY 10032, USA.*
**meg2008@cumc.columbia.edu*

from the retinal signal[3]. Sir Charles Sherrington supported Wundt's theory by hypothesizing that nerve endings on our extraocular muscles sense eye position (proprioception) and create a signal that is used by the brain to achieve spatial localization, "inflow"[4]. This is supported by the fact that in total darkness, humans report the sensation of passive changes in eye position, suggesting that our brains have access to an eye position signal[5].

An accumulation of evidence suggests that the two mechanisms proposed by Helmholtz and Sherrington are both used by the brain. This review will describe how they are used by the brain to achieve spatial accuracy. We propose that spatial perception is not achieved by a single mechanism, but rather a combination of both corollary discharge and oculomotor proprioception.

## 2 The Double-Step Saccade Task

The double-step saccade task is a simple paradigm developed by Hallett and Lightstone to test the mechanisms behind accurate spatial perception[6]. In this task, two targets were flashed on a screen sequentially after fixation in a dark room. The subjects were asked to search for the two targets locations based on the sequence that they were flashed. The vector for the first saccade is the same as the retinal vector whereas the vector for the second saccade is different. To make the second saccade, the brain must somehow compensate for the effect of the first saccade. The retinal vector alone is not sufficient to describe the spatial location of the second saccade target (Fig. 1). Despite the inaccuracy of the retinal vector, subjects were able to locate the second target accurately. The authors concluded that "saccades are towards the physical positions of targets—which is only possible if retinal image position and eye position information are correlated".

## 3 Remapping

Corollary discharge (efference copy) is a copy of the motor command sent from the brain to the muscles. Unlike the motor command signal, the corollary discharge signal does not travel down to the muscles. Instead, it goes to other regions of the brain to notify them of the upcoming movement. Because the corollary discharge occurs at the same time as the movement signal, the brain is informed of the movement even before the movement begins. An example of corollary discharge is when you speak into a recording device. As you speak into the device, the motor production of your voice feeds back to your sensory system, informing you that you are the one speaking. However, if you play back your voice, you are aware that it is the device playing your voice, not you.

Bruce and Goldberg[7] suggested that monkeys can solve the double-step task without access to eye position, using corollary discharge only[8]. They recorded cell activities as monkeys performed the double-step task. In the no-saccade task, a stimulus flashed in RF and, unsurprisingly, neurons gave a visual response (Fig. 2a). Next, monkeys made a saccade to the same stimulus and the cell fired in a similar way (Fig. 2b). When monkeys made saccades to the stimulus location without the stimulus present (Fig. 2c), the cell did not discharge. Likewise, there was no significant activity when monkeys made saccade to the opposite direction of the RF (Fig. 2d). This showed that the cells were purely visual. Yet, when the monkeys performed the double-step task, two neural activity peaks appeared. One appeared after the first saccade and the other before the second saccade, despite the fact that no stimulus

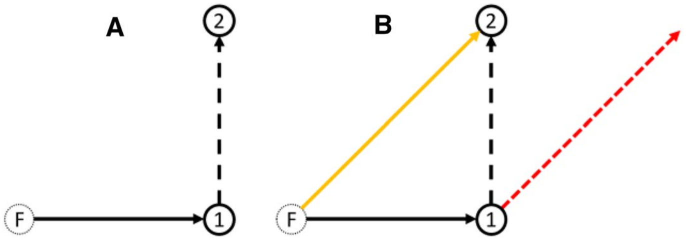

***Figure 1:*** Double-step saccade task: F is the fixation point, 1 is the first visually guided target, and 2 is the memory target. **a** Saccade vectors to the two targets. The visually guided saccade vector is denoted by the solid black arrow, while the memory-guided saccade vector is the dashed black arrow. **b** Shows the same task. The orange arrow represents the retinal vector to the second target. Without remapping, subjects will not be able to complete the second saccade accurately (red dashed arrow).

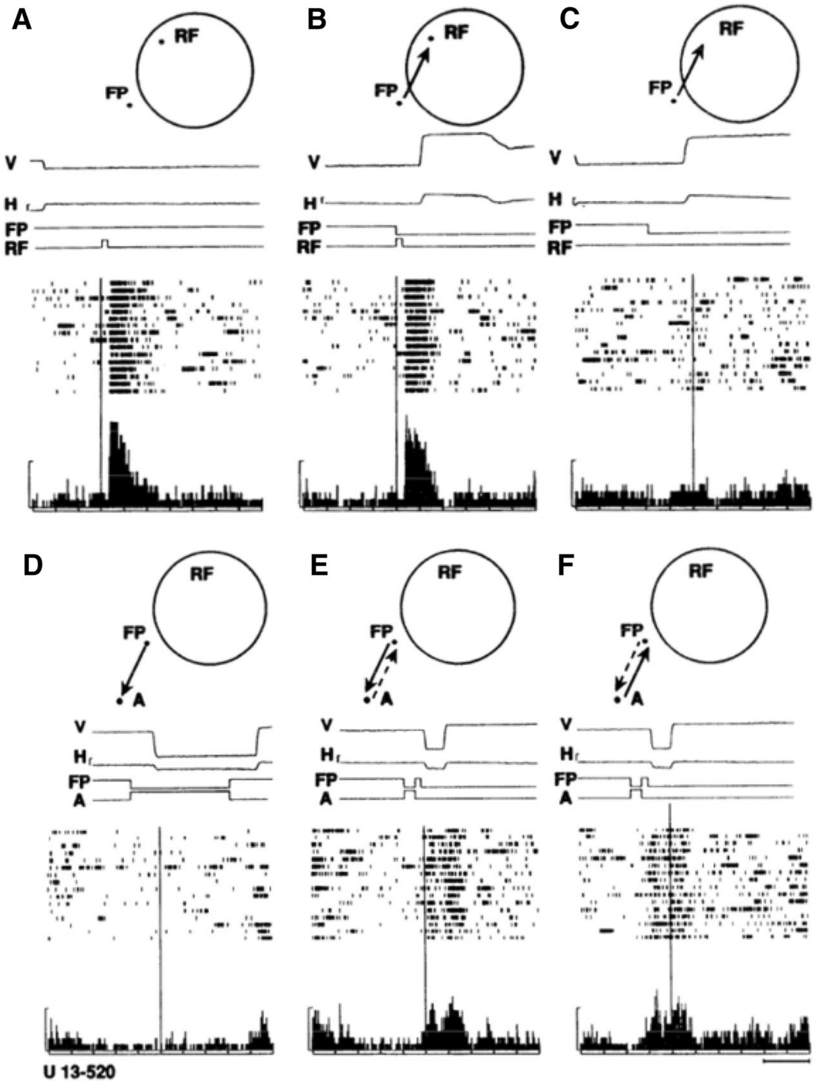

*Figure 2:* [8] Activity of visual cell without post-saccadic activity during no-saccade, consonant-vector, and dissonant-vector saccade tasks. **a** Neural response when stimulus flashed in the receptive field. Activity synchronized to stimulus onset. **b** Neural response when monkey made a saccade to stimulus in the receptive field. Note the similarity with (**a**). **c** Monkey makes a saccade into receptive field without a stimulus. There is a lack of visual response. Activity synchronized to start of saccade. **d** No visual response before or after when monkey makes a single saccade away from RF. Activity synchronized to end of saccade. **e** Brisk activity after the first saccade of in the double-step dissonant-vector task. Activity synchronized to start of first saccade. **f** Brisk activity before second saccade in double-step dissonant-vector task. Activity synchronized to start of second saccade.

was present in the RF (Fig. 2e, f). The authors proved two important findings. First, they showed that receptive fields are not static and can shift. The phenomenon was later termed receptive field remapping. Second, because the second activity peak occurred before the second saccade, it showed that proprioception was not necessary to solve the double-step saccade task.

Duhamel et al.[9] discovered that remapping occurs every time a monkey makes a saccade, not just in the context of the double task (Fig. 3). They studied neurons in the lateral intraparietal area (LIP). The cell gave a visual response to a stimulus in its receptive field (Fig. 3a). It did not respond when the stimulus flashed elsewhere in the visual field (Fig. 3b). It discharged before the saccade that would bring the spatial location of the stimulus FRF into the receptive field (Fig. 3c) but not when the monkey made the same saccade in the absence of a stimulus that would be

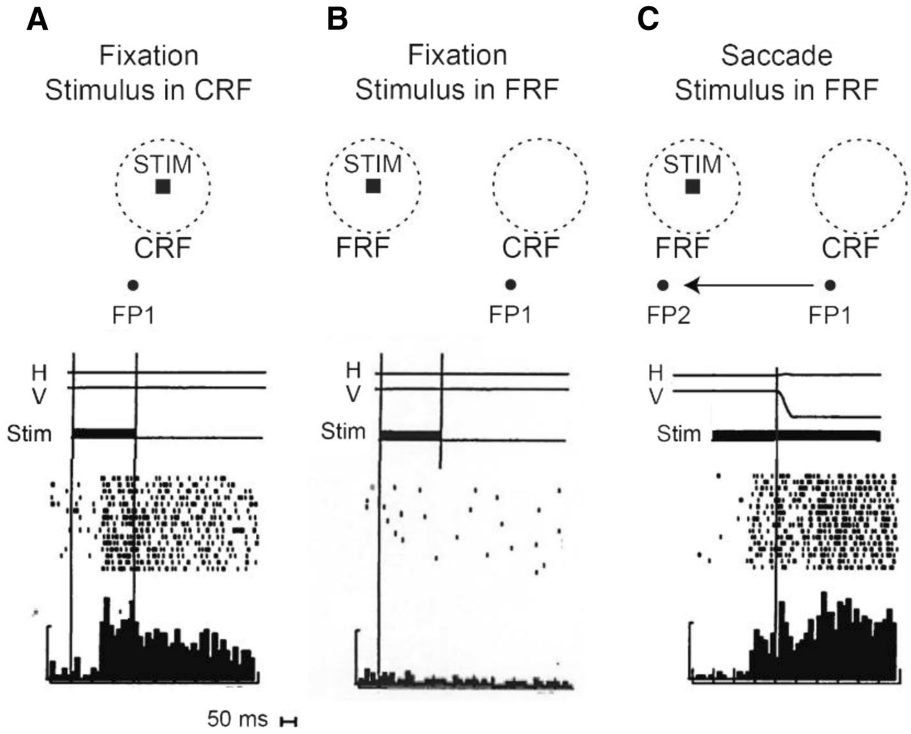

***Figure 3:*** (Adapted from Duhamel et al.[9]) Receptive field remapping in LIP. **a** Cell responds briskly to a stimulus appearing in its receptive field. Cartoon of the screen above: STIM visual stimulus. Dashed circle CRF, current receptive field. FP1 first fixation point. H and V, horizontal and vertical eye position. Stim, time of stimulus appearance. Raster diagram beneath: each dot is an action potential of the neuron. Each line is a trial. Trials synchronized on stimulus appearance (vertical line). The cell responds briskly. **b** Cell does not respond to a stimulus in the future receptive field (FRF). Conventions as in **a**. **c** Cell starts to respond before the saccade from FP1 to FP2 that will bring the saccade into its receptive field.

brought into its receptive field (not shown). Remapping is also present in many other areas, including the frontal eye field (FEF)[10], superior colliculus (SC)[11], the parietal reach region[12], and prestriate cortex[13].

To explain this perisaccadic shift further, Wang et al.[14] proposed three possible types of shifts: discrete shift, where the receptive field jumps from the current respective field to the future receptive field; continuous elongation, where the receptive field sweeps alongside the saccade trajectory; and non-specific expansion, where the receptive field expands until the saccade was made (Fig. 4a)[14]. To test these possibilities, the authors required monkeys to make a saccade from FP1 to FP2. During the saccade, a visual probe was flashed in 1 of 5 possible locations: the current receptive field (CRF) relative to FP1; the future receptive field (FRF) relative to FP2; an intermediate location (IML) placed between the CRF and the FRF; a mirror intermediate location (MIML); and a distal location (DL) placed beyond the FRF (Fig. 4b). They found that neurons in the receptive field responded to stimuli in the FRF, IML, and CRF locations around the saccade, but not to stimuli in the MIML or DL locations. This proved that the expansion is a continuous elongation along the part of the retina across which the saccade sweeps the receptive field. They modeled the remapping process as a wave of activity that sweeps across the cortex from the cells responding to the stimulus in the FRF to the cells that respond to a stimulus in the CRF. This wave only occurs when a corollary discharge enables the connections between adjacent cells in the cortex.

Sommer and Wurtz[15] showed that the corollary discharge signal that causes remapping in the frontal eye field (FEF) originates from the superior colliculus, where motor-related neurons activate saccades. The signals then travel through the medial dorsal nucleus of the thalamus (MD) and end at the FEF. The authors found presaccadic activity in MD[15]. They injected muscimol, a GABA agonist, in MD. The monkeys could still perform single visually and memory-guided

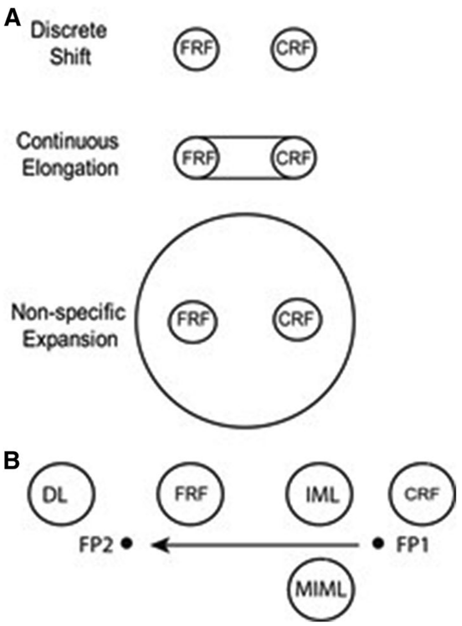

***Figure 4:*** [14] **a** Possibilities for receptive field expansion. For discrete shift, the cell can be driven by probe stimuli in the CRF and the FRF only. For continuous elongation, the cell can be driven by probe stimuli in the CRF and FRF, and along the retinal trajectory across which the saccade sweeps the receptive field. For non-specific expansion, the cell can be driven by probe stimuli beyond the limits of continuous elongation. **b** Experimental design. The monkey makes a saccade from FP1 to FP2. The probe stimuli were placed at one of five spatial locations: CRF; FRF; an intermediate location across which the saccade sweeps the retinal receptive field (IML); a mirror image location reflected across the saccade trajectory from the IML, which is not swept by the retinal receptive field (MIML); and a distal location (DL) extending beyond the FRF in the direction of the saccade, which is not reached by receptive field during the saccade.

saccades normally, but were unable to perform the second memory-guided saccade double-step task accurately.

## 4 Oculomotor Proprioception

The remapping phenomenon showed that Helmholtz's postulate of a corollary discharge provided a mechanism for spatially accurate behavior. Is there any role for eye position?

Andersen et al.[7] proved that visual activity in the lateral intraparietal area (LIP) of the rhesus monkey brain is modulated by eye position in a linear manner, monotonically increasing activity with the eccentricity of the eye in orbit (Fig. 5c)[7]. They referred to this eye position-dependent modulation as the gain field. In the experiment, monkeys were shown a target in their receptive field at nine different locations around the screen and performed a single visually guided saccade to each of them (Fig. 5a, b). They found that activity varied depending on the eye's orbital position, although the receptive field remained fixed to the retina. The source of the eye position signal was unknown, although Andersen et al. proposed that this signal was a corollary discharge of eye position.

Wang et al.[16] demonstrated the presence of an oculomotor proprioceptive signal in area 3a of the somatosensory cortex of monkeys. They found that these neurons represent the eye's position in the orbit, monotonically increasing with eye eccentricity just like the gain field[16]. These neurons represent all eye positions, not just contralateral ones. They then performed a retrobulbar block to inactivate the muscles and nerves in the orbit of one eye. They found that the block ablated the eye position signal in contralateral area 3a (Fig. 6). However, because the ipsilateral eye moved perfectly well, the activity that would have normally driven the inactivated eye must have been intact. This proved that corollary discharge was also unaffected. The eye position signal in area 3a lags the actual eye position by 60 ms[17]. The question then arose whether the eye position signal of the gain fields in LIP also lagged the eye position.

Xu et al.[17] showed that this is, in fact, the case. In this experiment, monkeys made a visually guided saccade, the conditioning saccade. A memory-guided saccade target then flashed at intervals between 50 and 650 ms after the conditioned saccade. Results showed that visual activity in LIP was modulated by the presaccadic eye position for targets flashed at 50 and 150 ms after the conditioned saccade[17]. This showed that gain fields were inaccurate at this interval. The authors then had the monkeys which perform the standard double-step task, flashing 50 or 650 ms after the conditioned saccade. Monkeys accurately completed the double-step saccade task when the targets flashed at 50 ms, even though the gain fields were inaccurate. The question then arose; are gain fields important at all?

There are some features of spatially accurate behavior that cannot explained by remapping. Karn et al.[18] asked subjects to make a saccade to a remembered target after 2 or 5 intervening saccades. They found that there was a little difference in saccadic error between the 2 and 5 saccade cases[18]. They argued that if a remapping mechanism was responsible for the accurate saccades to

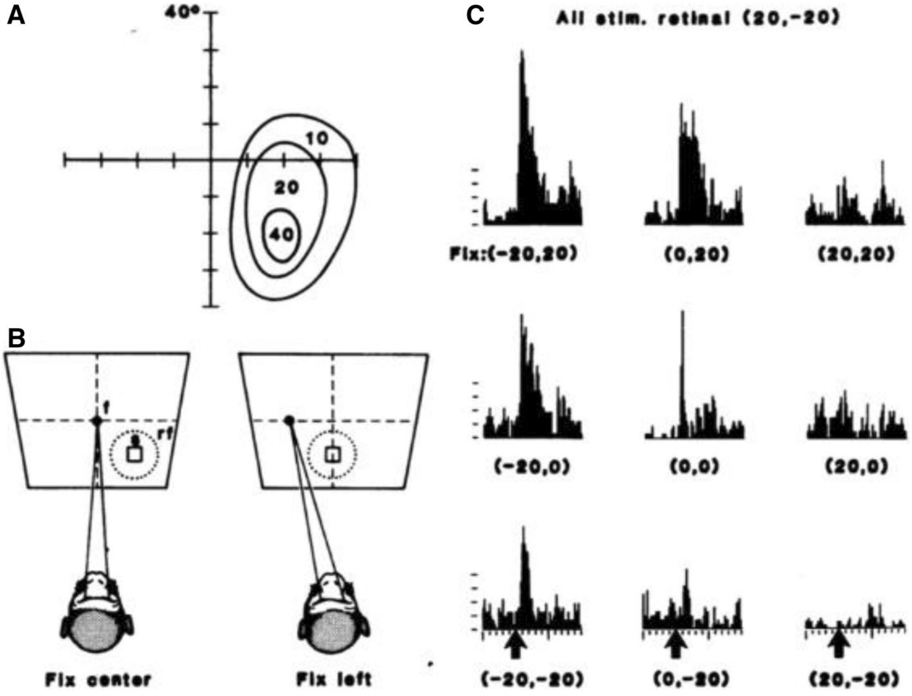

***Figure 5:*** [7] **a** Receptive field of a neuron plotted in coordinates of visual angle determined with the animal always fixating straight ahead (screen coordinates 0, 0). The contours represent the mean increased response rates in spikes per second. **b** Method of determining spatial gain fields of area 7a neurons. The animal fixates point f at different locations on the screen with his head fixed. The stimulus, s, is always presented in the center of the receptive field, rf. **c** Spatial gain field of the cell in **a**. Post-stimulus histograms are positioned to correspond to the locations of the fixations on the screen at which the responses were recorded for retinotopically identical stimuli presented in the center of the receptive field (histogram ordinate, 25 spikes per division, and abscissa, 100 ms per division; arrows indicate onset of stimulus flash).

a remembered target, the degree of error should increase as the number of saccades increased. Because this did not occur, they concluded that the brain established a craniotopic representation of the spatial environment, and accessing this head-centered representation did not entail repetitive errors (Fig. 6).

Poletti et al.[19] showed that both remapping and gain fields are required to explain all aspects of human spatial perception. They argued that if spatial representations are updated solely using corollary discharge to upgrade the retinal signal, then the variance in localization error should increase linearly as the number of intervening saccades increases. They asked subjects to make a memory-guided saccade to a target that briefly appeared before 1–9 intervening saccades. They found that for the first two intervening saccades, the variance in localization error increased linearly, suggesting that the subjects were using remapping[19]. After the third intervening saccade, the error variance started to become asymptotic. The authors modeled this by assuming that the brain starts to use a remapping mechanism and then gradually switches to a craniotopic mechanism (Fig. 7).

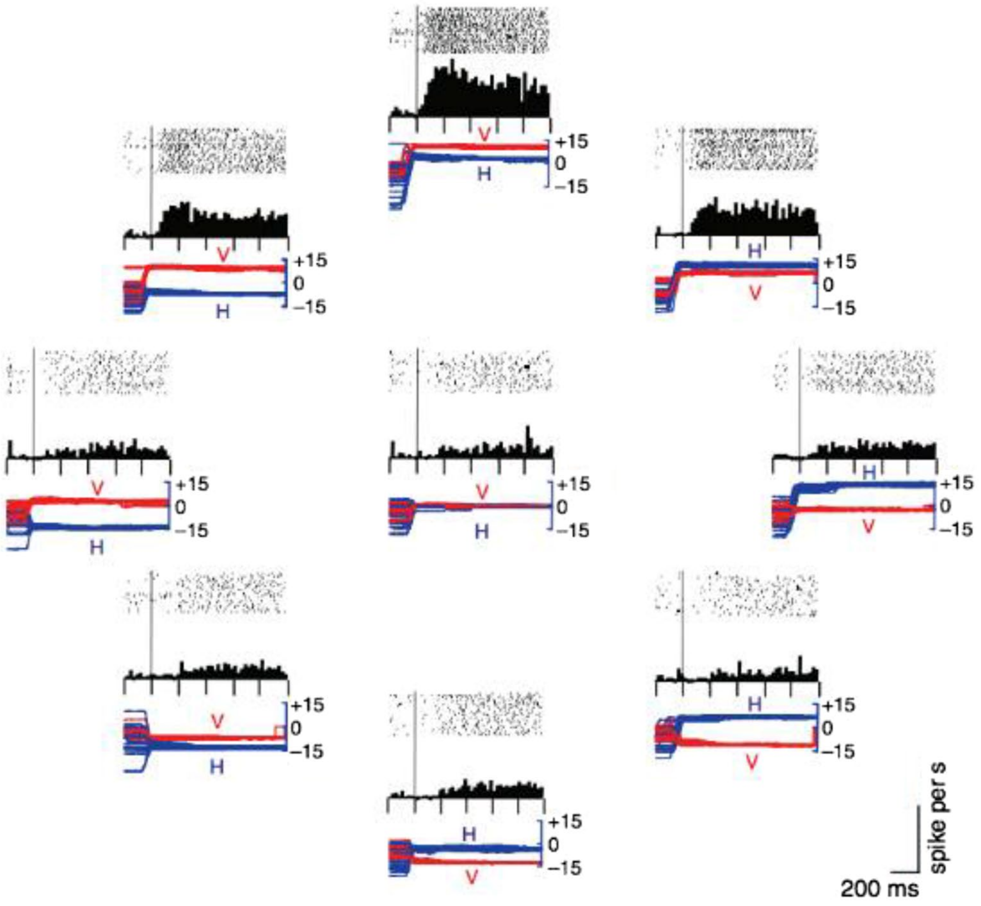

***Figure 6:*** [16] Activity of a tonic eye position neuron in monkey SI. Nine raster diagrams, one at the center of the orbit and eight others positioned radially 15 degrees from the center. The position of the raster is related to the position of the eye in the orbit. Each tick is an action potential, and each line is a trial. Lines are synchronized on the end of the foveating saccade. Because the trial began with the appearance of the fixation point, the eye position before the saccade was uncontrolled. The histograms beneath each raster average, without smoothing, the activity of the raster above, with a bin width of 25 ms. Eye positions for each trial are superimposed beneath each raster (horizontal, blue; vertical, red).

## 5 Conclusion

In this review, we have provided physiological evidence for two mechanisms by which the brain can create a spatially accurate representation of the visual world for perception and action: using a corollary discharge of an intended saccade to remap visual receptive fields (Helmholtz's theory) and a proprioceptive representation of eye position (Wundt's and Sherrington's theory). Remapping can precede the first saccade. Proprioception takes several hundred milliseconds after the saccade to be established. These two physiological mechanisms are consistent with the psychophysical evidence that the brain

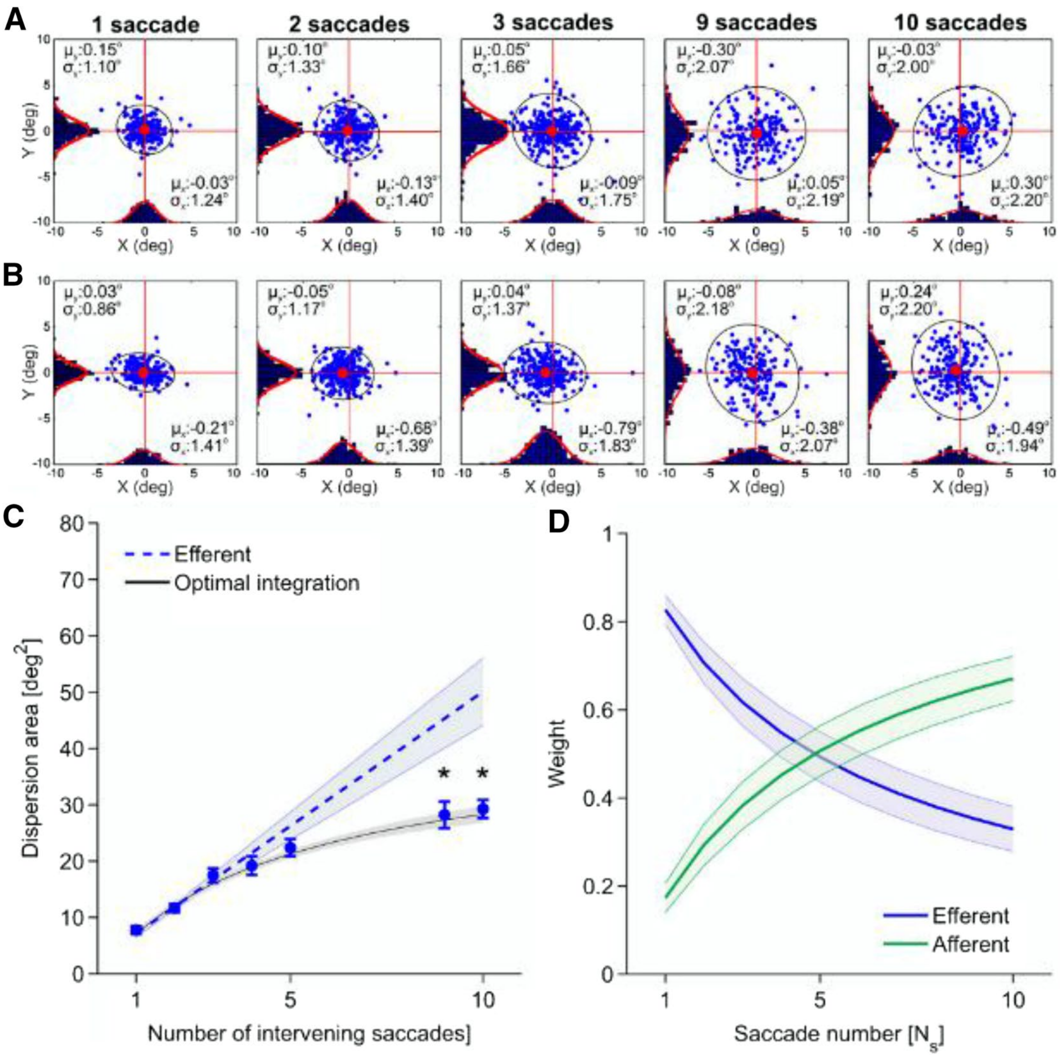

***Figure 7:*** [19] Visual localization (Experiment 1). **a** Summary of all trials. Each dot represents the localization error in an individual trial. Different panels show trials with different numbers of saccades between the target and the response cue. The mean error (red dot) and the 95% confidence ellipse are shown in each panel together with the marginal probability distributions and their best Gaussian fits, $N$ ($\boldsymbol{\mu}$, $\sigma$) (red curves). Data from all subjects ($N = 4$) were pooled together. **b** Same data as in **a** after rotating the axes to align the abscissa with the cue-target direction. **c** Mean dispersion area across subjects as a function of the number of saccades. Asterisks mark significant deviations ($p < 0.001$, two-tailed paired $t$ tests), from the predictions of a purely efferent estimate, as given by the linear regression of the measurements obtained with the first three saccades (blue line). The black curve represents the least-squares fit of the ideal observer model. **d** Optimal weighting of afferent and efferent estimates. As the number of saccades increases, proprioception is weighted more strongly and eventually becomes the predominant source of information. Error bars and shaded regions in **c** and **d** represent SEM.Z.

uses two mechanisms for locating a remembered target after intervening saccades, one whose error increases with the number of intervening saccades (consistent with remapping) and one whose accuracy stabilizes (consistent with the proprioceptive establishment of a craniotopic representation). As in many scientific debates, Helmholtz and Wundt were both right.

Despite the validity of these mechanisms, they do not paint a perfect picture of the visuospatial perception phenomenon. For example, Zivotofsky et al. showed that when humans and monkeys pursued a target moving orthogonally to a flow field, they perceive the target and their eyes to be moving diagonally[20], [21]. In fact, their eyes accurately follow the target, moving orthogonally to the flow field, as well (an example of this phenomena, called the Duncker illusion, can be found at https://www.youtube.com/watch?v=QUbJKakfmZw). When asked to make a saccade at the end of the task to a target that was flashed during the pursuit, subjects never made an accurate memory-guided saccade. They compensated for the diagonal movement they thought they had made. As a result, they overshot the target if the flow field moved toward the memory target or undershot when the flow moved away. This clearly shows that spatial perception does not rely solely on the eye muscle proprioception and remapping. Because of the Duncker illusion phenomenon, we propose that corollary discharge and oculomotor proprioception provide an accurate, but incomplete explanation for how exactly we perceive the world around us.

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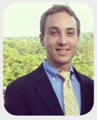

**Vincent Sanchez** grew up in Westchester, New York and is a graduate of the University of Michigan with a B.S in Neuroscience, and then began working for Dr. Goldberg at the Mahoney Center for Brain and Behavior Research at the New York Psychiatric Institute. After 1 year of working for Dr. Goldberg, he enrolled in the Institute of Human Nutrition at Columbia University. He recently submitted his thesis on spatial processing in the parietal lobe, and received his M.S. in nutrition. He is currently applying to medical school and working as a technician in Dr. Bijan Pesaran's lab at New York University.

**Wangzikang Zhang** or Zac is a graduate from the Macaulay Honors College at Hunter College. He is currently working in Dr. Goldberg's neuroscience research lab at Columbia University. There are two ongoing projects that Zac participates in. The first focuses on neuron recordings of gain fields in the lateral intraparietal cortex. The other looks at the somatosensory cortex (area 3a) and its role in oculomotor proprioception. By inactivating the somatosensory cortex of a rhesus macaque with a cooling probe, Zac found that the monkey began to show deficits of spatial accuracy to remembered target locations. The results were presented with a poster at the Gordon Research Conference (2017).

**Linus D. Sun** is an Assistant Professor of Neuroscience in Ophthalmology and Columbia. He is a board-certified neurologist. He is the recipient of a mentored NIH award to work in the Goldberg lab and study neuroophthalmology with Dr. Jeffrey Odel at Columbia.

**Michael E. Goldberg** is a Mahoney Professor of Brain and Behavior in the Departments of Neuroscience, Neurology, Ophthalmology, and Psychiatry at the Columbia University College of Physicians and Surgeons. He is a pioneer in the study of the physiology of cognitive processes in the awake, behaving Rhesus monkey. He is a clinical neurologist as well as a basic scientist.