The Need for Speed: Eye-Position Signal Dynamics in the Parietal Cortex

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Accurate eye-position signals are critically important for localizing targets in space when the eyes move. In this issue of *Neuron*, Xu et al. (2012) provide evidence that eye-position gain fields in area LIP remain spatially inaccurate for some time after a saccade, indicating they are not updated rapidly enough to play a role in the computation of target locations for upcoming saccades.

Human observers explore their visual environment using rapid gaze shifts called saccades. While saccades facilitate the efficient sampling of information across the visual field, they also impose a heavy computational cost on the brain. Many early visual neurons encode spatial information using eye-centered receptive fields whose positions are fixed relative to the retina. As a result, the information they convey depends on where the eyes are looking. Every change in eye position alters the retinal location of objects that remain fixed relative to the external world. This makes spatial localization following an eye movement challenging. One obvious solution is to discard information each time the eyes move, wait until the movement is complete, and then reacquire target locations based on (slow) visual feedback. However, we can localize a target in complete darkness even when an eye movement intervenes between the presentation of the target and its capture by a saccade, indicating that the brain does not exclusively rely on current visual information (Hallett and Lightstone, 1976). Instead, an internal signal representing eye position or eye displacement must be used in combination with retinal information to compensate for the eye movement. Various mechanisms have been proposed for how the brain performs this important computation. In the current issue of *Neuron*, Xu et al. (2012) investigate the temporal dynamics of eye-position gain fields in the lateral intraparietal area (LIP). They report that eye-position gain fields are inaccurate immediately following a saccade, yet strikingly, saccadic behavior during that

same interval remains accurate. From this, Xu et al. (2012) provocatively conclude that eye-position gain fields are not updated fast enough to be used by the brain to compute the location of targets for upcoming saccades.

Gain fields underlie a prominent model for how spatial information is handled by the brain. According to this model, the oculomotor system combines retinal target information and eye-position information together in a distributed, population encoding of supraretinal target location (Zipser and Andersen, 1988). The term "gain field" characterizes the way in which rate-coded postural signals (such as those carrying information about eye or hand position) interact with a receptive field or radial basis function (Poggio and Girosi, 1990). In particular, these rate-coded postural signals modulate the sensitivity or gain of an individual neuron's response without otherwise changing (i.e., shifting, broadening, or sharpening) the neuron's receptive field. For example, a neuron may be highly responsive when a visual stimulus is presented in its receptive field and the subject's gaze is to the right, yet respond only weakly when the same stimulus is presented in the receptive field and the subject's gaze is to the left. The overall pattern of modulation of visual responses over a range of different eye positions constitutes the neuron's gain field. Eye-position gain fields were first observed in areas 7a and LIP of the parietal cortex (Andersen and Mountcastle, 1983). They have since been described in a wide range of cortical and subcortical areas including V1, V3A, V4, V6A, MT/MST, VIP, PMd, SEF, SC, and the LGN.

The gain field model relies on population coding. Even though individual gain-modulated neurons receive the necessary inputs to represent target locations in supraretinal (e.g., head-centered) coordinates, this information is stored in a way that is ambiguous at the single-neuron level since many different combinations of eye position and retinal target location can give rise to the same neuronal response. The ambiguity is resolved by considering a population of neurons containing a broad distribution of gain fields and receptive fields. The representation of head-centered target information is thus implicit in the distributed population activity, rather than being explicitly represented by individual neurons with supraretinal receptive fields. An explicit representation by head-, body-, or world-centered neurons might appear to be a more efficient scheme than an implicit population encoding, since the explicit representation obviates the need for updating after each saccade, head, or body movement. However, behavioral and electrophysiological data reveal representations primarily based on eye-centered receptive fields (Baker et al., 2003; Colby and Goldberg, 1999), with only a minority of cells showing supraretinal encodings (e.g., Duhamel et al., 1997). The predominance of neurons with eye-centered receptive fields lends support to the gain field model.

A network using eye-position gain fields can be used to update visual information across saccades (Xing and Andersen, 2000). As noted above, when the eyes move between the presentation of the target and its capture by a saccade, there is a change in the

retinal location of the target. In an encoding scheme using eye-centered neurons, the population of active neurons must change after each eye movement. This change, the neural correlate of updating the retinal target location as a consequence of the eye movement, is referred to as "updating." Xing and Andersen (2000) proposed an extension of the gain field model to perform updating. Briefly, postsaccadic eye position signals are combined with a stored gain field representation of the pre-saccadic target location to compute a second, updated gain field representation of the target location. The gain field representation can subsequently be read out to provide either head-centered or eye-centered target information. Gain fields thus provide a unified model for how spatial updating occurs as well as for how a distributed encoding of eye- and head-centered target location may be implemented.

Despite the fact that gain fields have been implicated in both reference frame transformations (Pouget and Snyder, 2000; Zipser and Andersen, 1988) and spatial updating (Xing and Andersen, 2000), the evidence for their functional role is merely circumstantial. For example, neural network simulations confirm that gain fields are sufficient for computing supraretinal target locations, indirectly supporting a role for gain fields in the computation of target location (Zipser and Andersen, 1988). Recent findings from PRR provide additional support for a computational role for gain fields. Chang et al. (2009) report a highly systematic arrangement—a strong negative correlation—between eye- and arm-position gain fields within individual PRR neurons, the presence of which they argue is difficult to explain away as an inconsequential contaminant or noise. They suggest that "compound" gain fields encode the distance between the fixation point and the hand. This distance is exactly the variable required to transform eye-centered
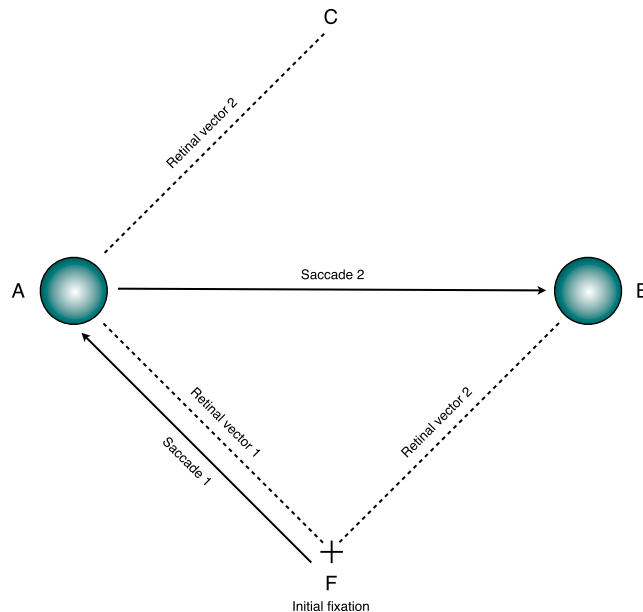

Figure 1. Double-Step Paradigm
Subjects begin by fixating an initial target (F) and must then perform successive saccades to two briefly flashed target locations (A then B). Retinal vectors 1 and 2 indicate the locations of targets A and B, respectively, at the time of visual presentation relative to fixation. Location C depicts the mislocalization error expected if information about the new eye position at A (following saccade 1) is not taken into account to program saccade 2, and instead only the original stored retinal vector from F to B is used.

visual target information into an arm-centered motor command for reaching. Nevertheless, direct evidence for a computational role of gain fields in neural circuits is difficult to obtain. Interventions to perturb or completely eliminate gain fields present technical challenges that are not easily overcome, and even worse, remain out of reach until we have a better grasp of the neural circuits and sensory inputs underlying gain fields.

A major strength of the current study is that it proposes a more direct experimental test of the computational role of gain fields than has hitherto been performed. Xu et al. (2012) asked if gain field modulations change rapidly enough to underlie spatial updating during a double-step saccade task. In the classic double-step paradigm (Figure 1), subjects are first instructed to maintain visual fixation on an initial fixation point (F) in an otherwise completely dark environment until the first saccade target (A) appears. The onset of A cues the subject to make the initial saccade from F to A. At some variable, randomly selected time after the onset of A, a second saccade target (B)

is briefly flashed at a different location, which the subject is permitted to acquire only after performing the initial saccade to A. Using a range of onset times for B guarantees that the target is presented either before, during, or after the first saccade (Hallett and Lightstone, 1976). Successfully acquiring the first target site is trivial and can be performed on the basis of stored retinal information alone, as the required saccade vector is just the stored retinal vector from F to A. Programming the second saccade is less straightforward if the eyes are no longer positioned at the same point as where the retinal coordinates for the second target were obtained. Consequently, if programming the saccade trajectory to the second target relies exclusively on the original stored retinal vector to the second target (vector F→B), that is, without updating for the new eye position, then the saccade will be inaccurate, ending at location C. Conversely, if the second saccade lands accurately at B, this demonstrates that the subject successfully compensated for the change in eye position. Psychophysical studies in humans (for review, see Ross et al., 2001) and monkeys (Baker et al., 2003; Dassonville et al., 1992) indicate that eye-position information is used to compensate for intervening eye movements during saccade programming, but that this compensation is imperfect or partial (perhaps due to an inaccurate eye-position signal), leading to localization errors when the targets for upcoming saccades are presented right around the time of a previous saccade. More specifically, localization errors occur whenever targets are presented from around 100 ms before to around 100 ms after saccade onset. The direction of the error also depends on when the target is flashed relative to the saccade. Targets presented just before a saccade are mislocalized in the same direction as the saccade, whereas targets presented just after the saccade are mislocalized in the opposite direction.

Xu et al. (2012) trained monkeys to perform a variant of the double-step task while they recorded from individual neurons in LIP, an area known to have eye-position signals and thought to be involved in saccade planning and spatial transformations related to saccades. More specifically, they quantified the amount of eye-position-dependent gain modulation in the visual responses to targets presented at various times (50–1,050 ms) following a previous saccade. They find that changes in gain field modulation lag the saccade by ∼150 ms. Despite this lag, saccade performance remained unaffected even when the saccade target appeared only during the time in which the gain field incorrectly reflected pre-saccadic rather than post-saccadic eye position (i.e., 50 to 150 ms after the end of the previous saccade). The authors reason that if an inaccurate eye-position gain field is used to compute saccade target location, then saccade behavior should also be inaccurate. The authors' striking observation of normal saccade performance despite inaccurate eye-position signals therefore provides evidence that gain fields are not—indeed cannot be—utilized in computing target locations for eye movements.

If gain fields are not updated rapidly enough to be used in neural computation, what is the alternative model? A signal indicating a change in eye position could be delivered to LIP and the updated vector computed in some other manner. It is clear that receptive fields are re-mapped (Duhamel et al., 1992; Colby and Goldberg, 1999). Nevertheless, the alternative to the gain field model has only been characterized in phenomeno-logical terms; a remaining challenge is to develop it into a mechanistic model (Mauk, 2000).

The specific version of the double-step task used by Xu et al. (2012) differs from the classic paradigm in an important respect that may have influenced their behavioral results. As previously mentioned, in the typical double-step paradigm, two saccade targets are presented sequentially in time with a distinct temporal gap between them. This design eliminates the presence of allocentric spatial cues that subjects could use to help localize the final saccade target. For example, if both saccade targets in

Figure 1 are presented simultaneously, then subjects might simply memorize the spatial relationship between A and B (e.g., B is to the right of A). After completing the initial saccade to A, subjects can then simply generate a saccade vector (A→B) that matches the stored allocentric representation of A and B. Indeed, Dassonville et al. (1995) demonstrated that the presence of allocentric spatial information during target presentation reduces (although does not completely eliminate) standard localization errors in the double-step task. It is then potentially problematic that Xu et al. (2012) employ a stimulus configuration that seemingly provides exactly this kind of allocentric spatial cue. In their version of the paradigm, both of the saccade targets (as well as the initial fixation target) were simultaneously present on the screen for a full 75 ms before the monkey was instructed to move. This additional spatial information could potentially improve accurate spatial localization performance and thereby mask mislocalization effects due to inaccurate eye-position signals. It could also explain why the findings reported by Xu et al. (2012) report smaller mislocalization errors in the double-step task than the rest of the literature.

Despite this caveat, the study provides an important challenge to our understanding of the role of gain fields in spatial representation and computation. A number of outstanding questions remain. First, are these findings robust across different cortical areas known to contain eye-position signals, or are they specific to LIP? Another recent study of gain field dynamics (Morris et al., 2012) shows similar lags for eye-position signals in LIP, such that most LIP neurons do not provide reliable information about eye position until around 200 ms after an eye movement. Interestingly, while this result is consistent with Xu et al. (2012), these results were not reproduced in nearby dorsal visual areas VIP, MT, and MST. Instead, eye-position signals in these areas appear to update much more rapidly, right around the time of the saccade and in some cases even slightly before the movement begins. These apparent inconsistencies in the temporal dynamics of gain fields across cortical areas produce a tension that requires

resolution. Nevertheless, caution must be exercised in drawing too strong a conclusion, since the paradigms differ in substantial ways: Morris et al. (2012) investigate eye-position modulation during static fixation, whereas Xu et al. (2012) examine modulation in response to a visual target.

A second outstanding question is whether the findings about the dynamics of eye-position gain fields in LIP apply to other motor systems or are specific to the oculomotor system. The authors imply that their findings have wide application, but this remains to be seen. Unique features of the oculomotor system could weigh against the extensibility of Xu et al.'s reported results. Most promi-nently, the oculomotor system—unlike many other motor systems—does not generally require an explicit computation of target location in supraretinal (e.g., head-centered) coordinates, since typi-cally only the retinal difference vector (the difference between the fovea and the retinal position of the target) is required for saccade programming. Consequently, the use or disuse of eye-position gain fields for computations related to saccade programming might not accurately reflect how other motor systems use them, especially where refer-ence frame transformations are required (Pouget and Snyder, 2000).

Finally, Xu et al.'s results should lead researchers in the field to reflect more broadly about what other roles (if any) gain fields might play in motor planning and sensorimotor transformations. Given their widespread presence throughout the brain, it is incumbent upon the field to embrace the purely negative answer that they play no functional role only as a last resort. Xu et al. (2012) hypothesize that the temporal properties of these eye-position signals, while unsuited for use in real-time saccade programming, might be deployed in a more ancillary way as a kind of feedback to calibrate motor efference copy signals.

Although major questions about gain fields remain open, Xu et al.'s inves-tigation of the temporal dynamics of eye-position gain fields in the lateral intra-parietal area (LIP) pushes us one step closer to understanding the role gain fields can—and cannot—play in neural computation.

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