Supplementary Materials for:

Journal of Neuroscience Volume X, pages X-X, 2011

Intrinsic reference frames of superior colliculus visuomotor receptive fields during head-unrestrained gaze shifts.

Joseph F.X. DeSouza[1,2,3,4,6*], Gerald P. Keith[1,3*], Xiaogang Yan[1], Gunnar Blohm[6,7], Hongying Wang[1], J. Douglas Crawford[1,2,3,4,5,6]

[1]Centre for Vision Research, [2]Neuroscience Graduate Diploma Program, [3]Department of Psychology, [4]Department of Biology, [5]School of Kinesiology and Health Science, York University, [6]Canadian Action and Perception Network (CAPnet), [7]Centre for Neuroscience Studies, Queen's University, Kingston, Ontario, Canada

---

Various topics associated with the PRESS method, developed in the Crawford lab, for identification of intrinsic reference frames of SC visuomotor receptive fields during head-unrestrained gaze shifts

Gerry Keith

1. Transforming target position and gaze direction between reference frames

Representing direction in 3-D

Direction in 3-D may be represented by a unit vector. Such a vector has only two degrees of freedom (since the third degree of freedom is removed by the vector having unit length), which may be represented as horizontal and vertical rotations from the straight-ahead direction. A right-handed orthonormal coordinate system in the lab-fixed reference frame may be defined where the straight-ahead direction lies on the positive x-axis, directly left is the positive y-axis and directly up is the positive z-axis (**Figure 1A**).

While a unit vector is completely described by the sizes of its y and z components in these coordinates alone – so that direction may be defined by a location on the y-z plane – this representation has the unfortunate property of being non-linear. A better approach is to represent the direction by the *quaternion* that will rotate the vector from the reference position, pointing in the straight-ahead direction, to the direction being represented. Quaternions have the form:

$$q = [q_0, \mathbf{q}] \tag{1}$$

where q_0 is the quaternion's *scalar component*, which is equal to the cosine of half the angle of rotation:

$$q_0 = \cos\frac{\theta}{2} \tag{2}$$

The quaternion's *vector component*, $\mathbf{q}$, lies on the axis about which the rotation occurs, $\hat{\mathbf{n}}$ (a unit vector), its length is equal to the sine of half the angle of rotation:

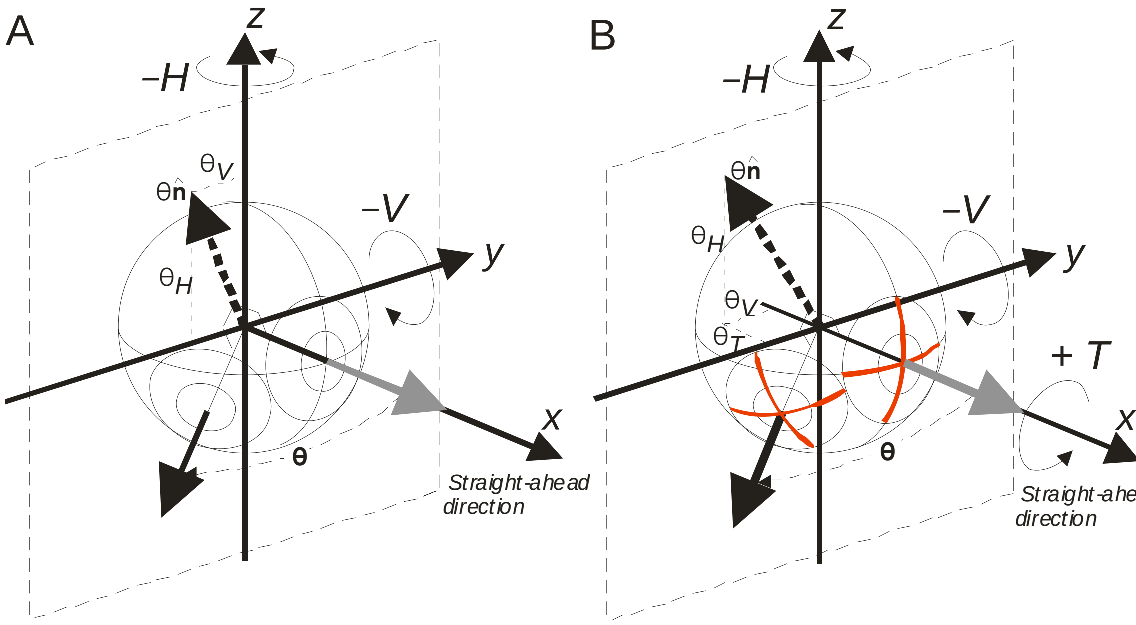

Figure 1 Representing gaze direction and eye position. A. A unit vector pointing in any direction in 3-D (black arrow) may be obtained from a vector pointing in the primary position direction (gray arrow) by rotating the latter by an angle θ about an axis lying in the plane perpendicualr to primary position (dashed black arrow). If this rotation axis vector has a magnitude equal to θ, then the horizontal and vertical components (θ_H, θ_V) define the components of the 2-D angle-vector representation of that direction. **B.** Eye position (orientation) involves not only gaze direction (black arrow) but the rotational component about gaze direction (indicated by the horizontal and vertical retinal meridians, the red cross). Eye position is obtained by rotating from primary position (gray arrow with upright red line meridians) about a rotation axis (dashed black arrow) that now does not necessarily lie in the plane perpendicular to primary direction. This rotation axis vector, given a length equal to θ, will in general have non-zero torsional as well as horizontal and vertical components (θ_T, θ_V, θ_H)., which define the 3-D angle-vector representation of eye position.

$$|\mathbf{q}| = \sin\frac{\theta}{2} \tag{3}$$

Thus, the overall form of the quaternion is:

$$q = \left(\cos\frac{\theta}{2}, \hat{\mathbf{n}}\sin\frac{\theta}{2}\right) \tag{4}$$

The vector component of the quaternion varies non-linearly with angle, θ, which is undesirable for graphical representations. However, a quaternion may be represented by an *angle-vector*, **AV**, which is scaled by the angle of rotation (**Figure 1A**):

$$\mathbf{AV} = \theta\hat{\mathbf{n}} \tag{5}$$

where:

$$\hat{\mathbf{n}} = \mathbf{q}/|\mathbf{q}| \tag{6}$$

and the rotation angle may be obtained from the scalar component of the quaternion (2):

$$\theta = 2\cos^{-1} q_0 \tag{7}$$

Each component of the angle-vector is the component of the overall rotation about the corresponding axis in the 3-D coordinate system. Since the rotations about all three axes are viewed as occurring simultaneously (performed by the quaternion), rather than in series as in the Fick or Helmholtz representations, angle-vectors have the useful property that all three component rotations are an equal footing. The horizontal rotation component is about the z-axis; the vertical rotation component is about y-axis, and the torsional rotation component is about the x-axis:

$$\mathbf{AV} = (\theta_T, \theta_V, \theta_H) \tag{8}$$

In representing a *direction* in 3-D, the most direct rotation of a unit vector initially pointing in the straight-ahead direction will be about rotational axis, $\theta\hat{\mathbf{n}}$, that lies in the y-z plane. Thus angle-vector representations of direction in 3-D will always have a zero torsional component, and may be represented as positions in 2-D (horizontal and vertical) *angle-vector space*. For example, the direction (position) of a target may be defined by:

$$\mathbf{T} = (\theta_H, \theta_V) \tag{9}$$

Representing orientation in 3-D

Orientations in 3-D may not in general be represented by 2-D angle-vectors. Consider head orientation. If its primary orientation is upright and facing in the straight-ahead direction, any change in orientation may include not only horizontal and vertical rotations, but torsional rotations (head tilt) as well. Thus, in general, orientations in 3-D may have all three components that are non-zero (**Figure 1B**), as indicated in (8).

Note that the angle-vector representation is useful only in *picturing* orientation. The quaternion (1) associated with the orientation must be used to perform transformations. Angle-vector and quaternions are related by (1-7).

Representing gaze as a direction in 3-D

Note that *gaze orientation* (i.e., eye orientation-in-space), is an orientation in 3-D with in general non-zero vertical, horizontal and torsional components, and must be represented by a quaternion (rather than a vector). *Gaze direction*, on the other hand, which defines the *direction of regard* (the arrow that points out of the eye towards whatever is being foveated), is a direction and may be represented by a unit vector. Gaze direction has only two degrees of freedom, and does not take into account the degree of freedom of eye rotation about the direction of regard.

The gaze direction unit vector may be obtained by rotating a unit vector initially pointing in the reference, straight-ahead direction by the quaternion representation of gaze orientation. Note that the algebraic description of this that is given here works equally well for *any* direction, that is gaze or target direction (position) in 3-D.

If the reference unit vector points in the straight-ahead direction (along the positive x-axis) it will be:

$$\mathbf{V}_0 = (1,0,0) \tag{10}$$

Since quaternions multiply only with other quaternions, a 'scalar' component, having a zero value, must be added to this vector, the result, $[0,\mathbf{V}_0]$, having the four-component form similar to a quaternion. The rotation of the vector by a quaternion, q, is:

$$[0,\mathbf{V}] = q\,[0,\mathbf{V}_0]\,q^{-1} \tag{11}$$

where $\mathbf{V}$ is the rotated 3-D unit vector, and q^{-1} is the inverse of the quaternion, which is:

$$q^{-1} = [\mathrm{q}_0,-\mathbf{q}] \tag{12}$$

Quaternion multiplication takes the form:

$$r = p\,q \tag{13}$$

where the components of the product are defined by:

$$\begin{aligned} r_0 &= p_0 q_0 - \mathbf{p}\bullet\mathbf{q} \\ \mathbf{r} &= p_0\mathbf{q} + \mathbf{p}q_0 + \mathbf{p}\times\mathbf{q} \end{aligned} \tag{14}$$

and × and • represent the standard cross and dot products of vectors.

Thus gaze direction, **Gd**, may be obtained by rotating a unit vector pointing in the reference straight-ahead direction, $\mathbf{V}_0$, by the quaternion form of gaze orientation, q_G:

$$[0,\mathbf{Gd}] = q_\mathrm{G}\,[0,\mathbf{V}_0]\,q_\mathrm{G}^{-1} \tag{15}$$

Performing transformations between reference frames

In order to perform regression fits of the neural activity in different reference frames, the spatial quantity must be transformed into the proper reference frame. The two spatial quantities examined in this study, visual target position, **T**, and final gaze direction, $\mathbf{Gd}_f$, represented by unit vectors in 3-D, may be transformed from the reference frame in which they are defined (which is lab frame, termed "space frame") into head frame, for example, by rotating by the inverse of the quaternion representing head orientation:

$$[0,\mathbf{T}_H] = q_H^{-1}\,[0,\mathbf{T}_S]\,q_H \tag{16}$$

$$[0,\mathbf{Gd}_{f/H}] = q_H^{-1}\,[0,\,\mathbf{Gd}_{f/S}]\,q_H \tag{17}$$

where $\mathbf{T}_H$ and $\mathbf{Gd}_{f/H}$ are the target position and final gaze direction in head frame, represented as 3-D unit vectors.

The rationale for this may be understood intuitively by imagining the position quantity as a point in 3-D space relative to a orthonormal coordinates system representing space frame. A second set of orthonormal coordinates (say head orientation) has the same origin as the first but is rotated in an arbitrary way relative to it. The position of the target relative to the second set of coordinates may be understood as *removing the head orientation*, that is by rotating the second set of coordinates *along with the position point*, until that set of coordinates is identical to the first set of coordinates. The position point relative to the coordinate system is now the target position in head frame.

A similar formula is used to convert target position and final gaze direction from space into eye frame, this time by rotating by the inverse of the *initial* gaze orientation:

$$[0,\mathbf{T}_E] = q_{Gi}^{-1}\,[0,\mathbf{T}_S]\,q_{Gi} \tag{18}$$

$$[0,\mathbf{Gd}_{f/E}] = q_{Gi}^{-1}\,[0,\,\mathbf{Gd}_{f/S}]\,q_{Gi} \tag{19}$$

Transforming into fixed-vector eye frame

Fixed-vector eye frame differs from the other frames we have used, in that it is reached by performing a *translation* in angle-vector space. (This is still a rotation in ordinary space, since angle-vectors represent directional quantities, but not a rotation about a fixed axis.) In this transformation, from the 2-D angle-vector representation of the direction in space frame is subtracted the initial gaze direction, again represented as a 2-D angle vector.

Converting between unit vectors, quaternions, and angle vectors

Given any gaze position or target direction represented as a unit vector, we can generate a quaternion of rotation that produces this vector from a unit vector in primary position (along the positive x-axis) through angle θ about an axis that lies in the y-z plane. If the components of the unit vector **V** are:

$$\mathbf{V} = (x, y, z) \qquad (20)$$

then, without showing the details of the derivation, the components of the quaternion that performs this rotation and which has a zero torsional component, are:

$$q = \left(\sqrt{\frac{1+x}{2}}, 0, \frac{-z}{\sqrt{2(1+x)}}, \frac{y}{\sqrt{2(1+x)}} \right) \qquad (21)$$

To convert this quaternion into an angle vector representation, simply apply the equations (5) to (7). To convert an angle vector into a quaternion, take the angle vector in the form:

$$AV = (\theta_T, \theta_V, \theta_H) \qquad (22)$$

and apply:

$$q = [\cos(\theta/2), (\theta_T/\theta)\sin(\theta/2), -(\theta_V/\theta)\sin(\theta/2), (\theta_H/\theta)\sin(\theta/2)] \qquad (23)$$

2. Intermediate reference frames

The algebra of intermediate reference frames in 3-D

A continuum of intermediate reference frames may be defined, anchored by two canonical reference frames (such as space and eye frame), may be defined by a parameter, α_{SE}. This parameter measures the fraction of rotation from the first frame towards the second. Thus in the space-to-eye frame continuum $\alpha_{SE} = 0$ corresponds to space frame, and $\alpha_{SE} = 1.0$ corresponds to eye frame. Parameter values beyond the interval zero-to-one define frames that lie beyond these two frames.

To rotate either a target position or gaze direction into any intermediate reference frame, begin with that 2-D direction in one of the canonical reference frames that anchor the continuum. For example, gaze direction in space frame. The quaternion representing the rotation from space to the second canonical frame defining the continuum, in this case eye frame, q_{SE}, is calculated, as was detailed in the previous section. To calculate the quaternion that will rotate from space frame to any intermediate frame defined by a certain α_{SE} value, one merely modifies the formula for the quaternion given in (4) by this value:

$$q = \left(\cos\frac{\alpha_{SE}\theta}{2}, \hat{\mathbf{n}}\sin\frac{\alpha_{SE}\theta}{2} \right) \tag{24}$$

This is most easily done by converting the quaternion in question into a 3-D angle vector, multiplying each component of this by the parameter α_{SE}, and then transforming the new angle-vector back into quaternion form.

For intermediate frames along continuums anchored by fixed-vector eye frame, the transformation from the other canonical anchoring frame to the intermediate frame comprises not a rotation but a translation, as described in the previous section. The direction of a given trial in both canonical frames is computed as 2-D angle vectors. The 2-D vector pointing to the fixed-vector eye-frame position from the other canonical frame position is then scaled by the α-parameter value and added to the non-fixed-vector frame position.

An example trial plotted in all canonical and intermediate reference frames

Figure 2A shows actual data from a representative trial, the initial and final gaze (red) and head (green) directions in terms of 2D angle vectors (that is, in terms of horizontal and vertical rotations from the straight-ahead direction). Everything is represented in terms of space (i.e., lab) frame. As can be seen, initial and final gaze and head directions point in quite different directions, and that both are substantially different than the straight-ahead direction (the origin). This means that the saccade-target position (blue box) will be in quite different directions in space, head, and eye frames. Also note that the final gaze direction (red circle) is quite different from the saccade-target direction, reflecting the fact that the monkey was given a wide range of tolerance. This will continue to be reflected in all reference frames, so that final gaze and saccade-target positions will be different in each of the space, head and eye frames.

Figure 2B shows the final gaze direction for the same example trial, plotted in the four canonical reference frames of space (Gs), head (Gh), eye (Ge), and fixed-vector eye (Gv), as well as in intermediate frames between and beyond these frames along the 6 continuums connecting the four frames, with the parameter values α taking values between -0.5 and 1.5 in 0.1 intervals (and values of 0 and 1.0 represent the two canonical frames associated with the continuum in question). The positions in continuums involving the fixed-vector frame are shown as small blue dots, and it may be seen that these are related by a linear translation in 2-D angle-vector coordinates. The positions in continuums not involving the fixed-vector frame are shown as small black dots, and are related by curves reflecting the fact that orthogonal angle-vector space does not represent true rotations in 3-D space.

Figure 2C shows the saccade-target direction for the same trial, plotted again in the four canonical and intermediate frames, space (Ts), head (Th), eye (Te), and fixed-vector eye (Tv), using the same conventions as in **Figure 2B**.

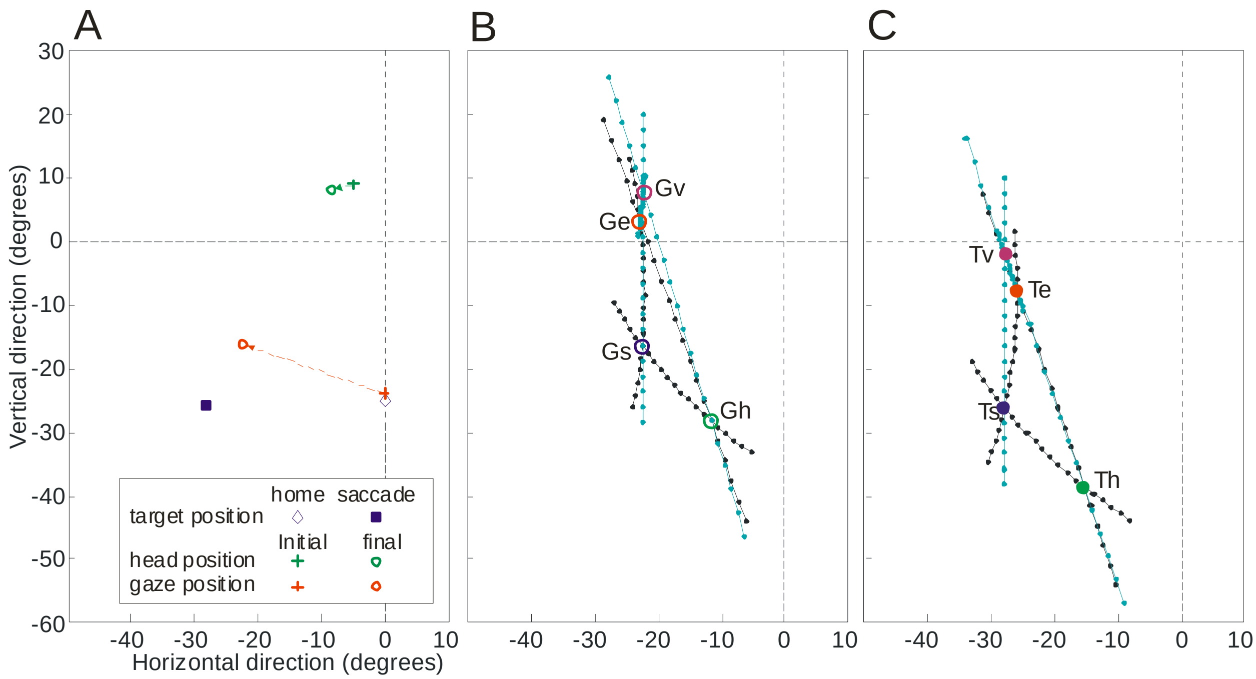

Figure 2 Target and final gaze positions in intermediate reference frames. A. Home- and saccade-target positions are plotted in 2-D for a single trial from an example neuron along with initial and final 2-D gaze (eye-in-space) and head directions. **B.** Final gaze directions for the example trial in space (Gs), head (Gh), eye (Ge), and fixed-vector eye (Gv) frames, as well as intermediate reference frames on continuums between and beyond pairs of these frames. (Positions on continuums involving fixed-vector eye frame are in blue.) **C.** Saccade-target positions for the example trial in space (Ts), head (Th), eye (Te), and fixed-vector eye (Tv) frames for the example trial are plotted for the same reference frame continuums as B.

3. Dealing with widely-spaced trials

A subset of the neurons in our data set involved three widely-spaced home-target positions, each having saccade-target positions that similarly placed relative to the home-target position. This produced an artifact which biased the test of intrinsic reference frame *against* frames close to eye frame. The reason for this is as follows.

When saccade-target or final-gaze positions plotted in eye frame, the three subsets corresponding to the trials associated with each of the three home-target positions overlap because, as already stated, the saccade-target positions relative to home-target position are the same for all three home-target positions. When saccade-target or final-gaze positions are plotted in space frame, however, they are quite separate (*as seen in the paper proper:* ***Figure 6A***). When plotted in head frame, on the other hand, there is *partial* separation of these three data subsets. This is because the initial head position tends to move part-way towards the initial, home-target position for the different trials.

The position separation of data subsets in space frame (and partial separation in head frame) means that the firing rates measured in trials in the different subsets do not interact in terms of the fitting routine in space frame, since they are distant from each other (or have reduced interaction in head frame). This has the effect of artificially reducing the PRESS value for the data plotted in space frame, and slightly reducing it in head frame. This reduction in turn *biases* the test used to identify the frame with the smallest PRESS as the neuron's intrinsic reference frame – biases it *towards* space frame and *away* from eye frame.

This is shown schematically in **Figure 3**, where the PRESS for three neurons are shown for intermediate reference frames along a continuum between and beyond space and eye frames (alpha = 0 corresponding to space frame, alpha = 1.0 corresponding to eye frame). The intrinsic reference frame of each neuron (indicated by the vertical gray arrow) is, respectively, space (panel A), midway between space and eye (panel B), and eye (panel C) frame. The effect of these intrinsic reference frames alone (dashed black line) is a reduction in the PRESS value for

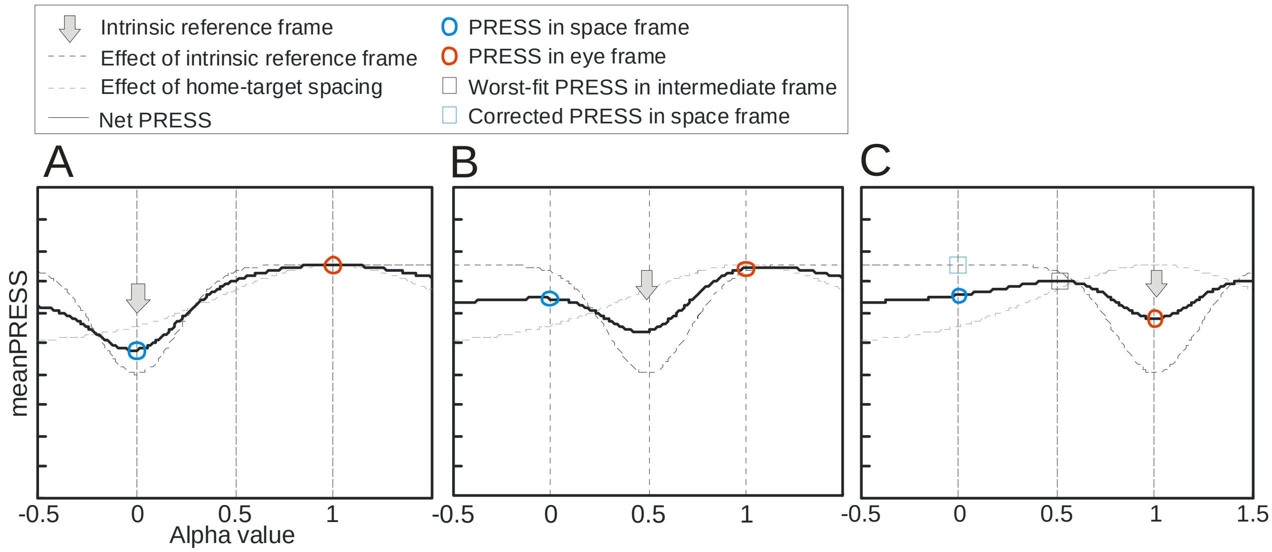

Figure 3 Interaction between the intrinsic reference frame and the artifact from using 3 widely-spaced home-target positions. When data using 3 widely-spaced home targets is used, the effect of spatial coherence on the PRESS statistic by which the intrinsic reference frame is identified (black dashed line) is contaminated by an artifact that lowers the PRESS away from eye frame (gray dashed line), producing a measured PRESS value that is suppressed for intermediate reference frames approaching space frame (black solid line). These are shown for intermediate reference frames between and beyond space and eye frame when the intrinsic reference frame (gray arrow) is (**A**) space frame, (**B**) halfway between space and eye frame, and (**C**) eye frame. When the intrinsic reference frame is eye frame (**C**), the measured PRESS has a maximum PRESS at an intermediate frame (”) that is larger than the PRESS at either space (❹) or eye (❹) frame. This intermediate worst-fit PRESS represents a partial correction for the artifact, being more conservative (smaller) than the PRESS in space frame with the artifact removed entirely (”).

frames close to the neuron's intrinsic reference frame (this is the central underpinning of our PRESS method). Also shown in this figure, however, is the artifact that arises from the use of three widely-spaced home-target positions, which increases PRESS for frames close to eye frame (dashed gray line). In these examples the *measured* PRESS will simply be the average of these two effects. (Note: for actual neuron data the combination of the effects can be non-linear, and will vary due to many factors. Importantly, however, they will be directionally similar to what has been shown here.)

For the neurons whose intrinsic reference frame is space frame (panel A), or midway between space and eye frame (panel B), the measured PRESS for intermediate frames *between* space and eye frame are either monotonic (panel A), or show a minimum partway along (panel B). When the neuron's intrinsic reference frame is eye frame (panel C), however, the PRESS shows a local maximum partway along this continuum (□), which is larger than the PRESS in either space (blue ○) or eye (red ○) frame. The existence of this maximum PRESS at an intermediate frame along a continuum involving space (or head) frame therefore indicates that the intrinsic reference frame lies towards the other canonical frame (eye frame).

The importance of this observation lies in the ability to discriminate space frame and the other canonical (most likely eye or fixed-vector eye) frame. With the PRESS in space frame artificially lowered from its correct value (blue □) to the measured value (blue ○), the *difference* between the PRESS in space and eye frame is reduced, producing a statistical *p*-value for the test between these frames that is *less significant*.

A correction for this artifact was to approximate the correct space frame PRESS (which cannot be measured) using the intermediate frame maximum PRESS. This has the effect of reducing the artifact arising from the three home-target positions, and thus improves the *p*-value of the statistical test between space and eye frame. It is important to remember that the *p*-value of the t-test using this replacement space-frame PRESS will be *less significant* than that if the correct space-frame PRESS values were used. This correction, therefore, is conservative and produces a *p*-value relative to which one may say the (unmeasurable) correct *p*-value *must be* more significant.

An example of this procedure used on an actual neuron is shown in Supplementary **Figure 4**. The mean (transformed) PRESS values of the fits of final gaze position in intermediate frames on the continuums between and beyond space and eye frame (black), and space and

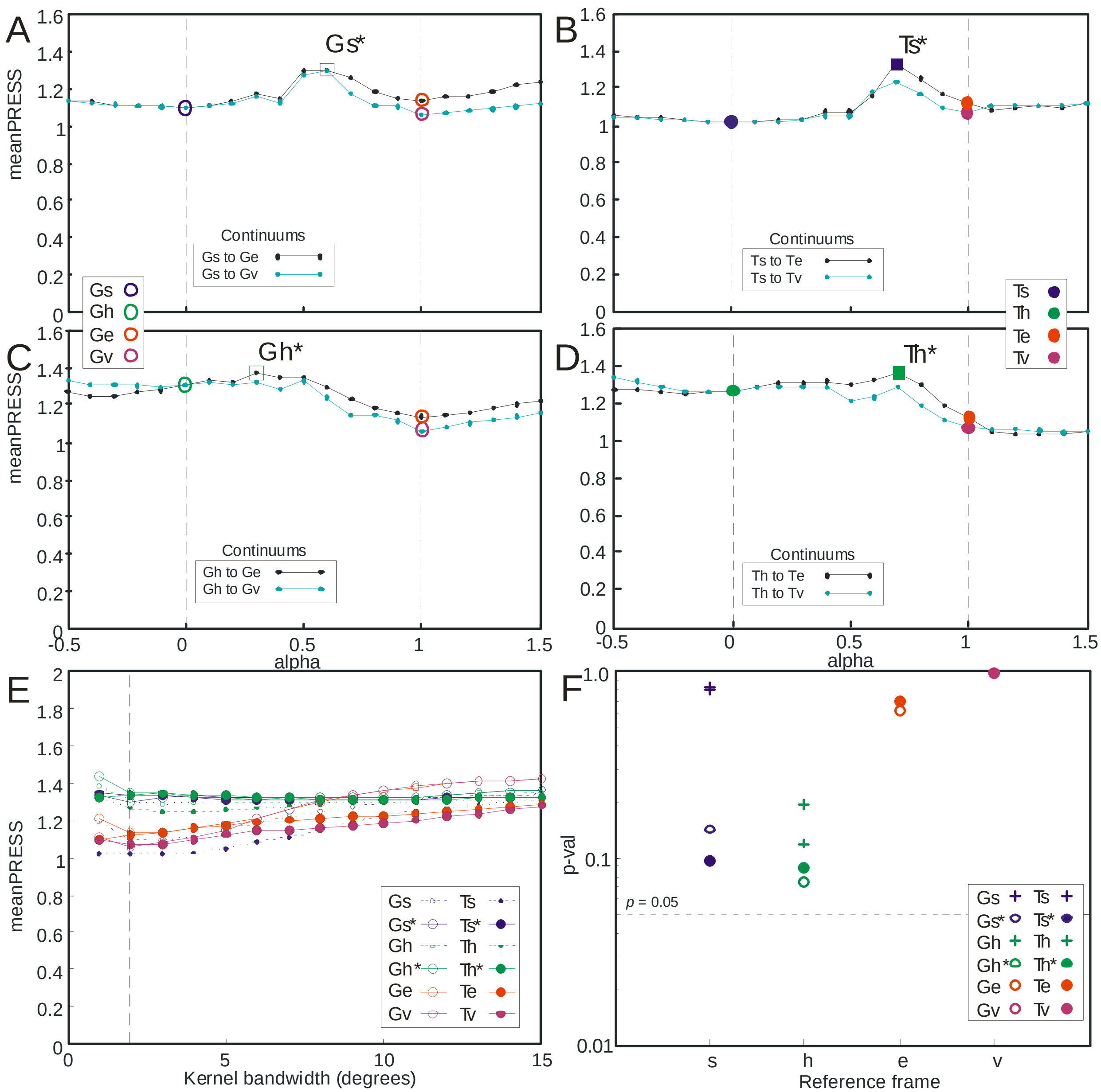

Figure 4 Example neuron PRESS and *p*-values for which the artifact due to the use of 3 widely-spaced home-target positions has been removed. The root-mean-square (RMS) PRESS are plotted for the intermediate reference frame continuums between and beyond space and eye for final gaze (**A**) and target (**B**) positions, and for continuums between head and eye for final gaze (**C**) and target (**D**) positions. The continuums involving eye frame proper (e) are in black, while those involving fixed-vector eye frame (v) are in blue. The PRESS of the intermediate frame with the largest PRESS in each panel, that will replace the PRESS of the canonical frame to the left is indicated by a star (*). For example, in panel A the intermediate PRESS Gs* will replace the canonical final-gaze-in-space frame, Gs. **E** shows the PRESS for the final gaze (G) and saccade-target (T) positions plotted in the canonical frames: space (s), head (h), eye (e) and fixed-vector eye (v) for all kernel bandwidths. Also shown are the PRESS for the replacement intermediate frames, indicated by a *. **F** shows the *p*-values comparing the PRESS of all canonical frames and replacement frames with the best-fit canonical frame (target in fixed-vector eye frame). The effects of a linear gain field with coefficient 0.014 has been removed from the data prior to fitting.

fixed-vector eye frame (blue) are plotted in **Figure 4A**. The overall intermediate frame between the pairs of canonical anchor frames for which PRESS is a maximum is indicated (Gs*). A similar intermediate maximum PRESS is observed for saccade-target position plotted in the same continuums is indicated (Ts*) in **Figure 4B**. **Figures 4C** and **4D** show the similar results obtained for final-gaze and saccade-target positions along the continuums between head and eye/fixed-vector-eye frames. These intermediate frame PRESS values replace the PRESS for canonical space and head frames, and the mean PRESS are shown for original (dashed lines) and replacement PRESS for fits at all kernel bandwidths from 1 to 15° in **Figure 4E**. Once the original space and eye frame PRESS values are eliminated, the best-fit PRESS is at kernel bandwidth of 2°, for target in fixed-vector eye frame. Using this frame as the best-fit frame, 2-tailed t-tests comparing the PRESS in this frame with each other frame yield *p*-values shown in **Figure 4F**. Using the replacement space and head PRESS values (circles) rather than the original PRESS values (+) produces *p*-values that are much closer to being significant. The actual *p*-values that would have been obtained without the artifact due to the three home-target positions altogether would have been more significant, but since these values cannot be measured, the replacement *p*-values must remain the upper limit of the former.