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Mechanical interdependence of version and vergence eye movements

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Abstract In this paper, the authors investigate whether the idea of independent control of version and vergence eye movements is compatible with the mechanics of the eye plant. By computing the change in the axes of action of the eye muscles as a function of ocular vergence, they prove that, regardless of the muscle pulley locations, the required muscle activity for vertical version depends on the initial vergence angle.

The binocular extension of Listing's law ('L2') describes how the torsional orientation of the eye depends on both gaze direction and ocular convergence. The authors show that for each vergence angle there is a range of possible muscle pulley locations that would cause independent control of version and vergence to result in L2. They also show that this mechanical explanation of L2 requires that the muscle pulleys move as a function of vergence.

Key words Listing's law; muscle pulleys; vergence; version; modeling

Introduction It is generally assumed that version and vergence eye movements are controlled by distinct neural systems implementing Hering's law of equal innervation.[1] In this architecture, the vergence system is concerned only with the fixation distance and the version system is concerned only with the (cyclopean) gaze direction. This idea is supported by neurophysiological data which indicate that the signals for version and vergence eye movements come from different areas in the brain.[2]

Even though the version and vergence signals originate in different areas of the brain, both are ultimately sent to the same 12 muscles of the two eyes (six per eye). Mechanically, independent control of version and vergence movements is, therefore, only possible if the axes of action (i.e. unit moment vectors) of the extraocular muscles (EOMs) do not change as a function of eye orientation. Based on principles of 3D rotation we will determine how the axes of action of the EOMs

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depend on the orientation of the eye and how this affects the control of version and vergence movements. First, we prove that, regardless of the location of the muscle pulleys, the axes of action of the EOMs change as a function of vergence. Then we show that this interdependence between version and vergence movements may be the cause of the tilt in Listing's plane that has been found as a function of vergence (binocular extension of Listing's plane[3]), provided that the muscle pulleys are located at the appropriate positions and move with vergence.

Materials and methods

COMPUTATION OF THE AXIS OF ACTION OF A MUSCLE The EOMs follow the shortest path from their insertion point (**I**) on the eye to a position in the eye socket, designated as the effective muscle pulley location (**P**), that serves as the functional mechanical origin of the muscle.[4,5] To simplify the calculations, the following two assumptions were made: the globe of the eye was modeled as a perfect sphere with the center of rotation at the center of the sphere and the muscle paths were modeled as lines rather than bands.[6–11]

Using a head-fixed coordinate system centered on the eye, the vectors $\vec{\mathbf{I}}_i$ and $\vec{\mathbf{P}}_i$, determining the insertion point and pulley position of the ith EOM, span the plane of the shortest muscle path between $\vec{\mathbf{I}}_i$ and $\vec{\mathbf{P}}_i$ (Figure 1).

Using a right-handed coordinate system, the axis of action ($\hat{\mathbf{M}}$) of an EOM is therefore determined by:

$$\hat{\mathbf{M}}_i = \frac{\vec{\mathbf{I}}_i \times \vec{\mathbf{P}}_i}{\left\| \vec{\mathbf{I}}_i \times \vec{\mathbf{P}}_i \right\|}, \tag{1}$$

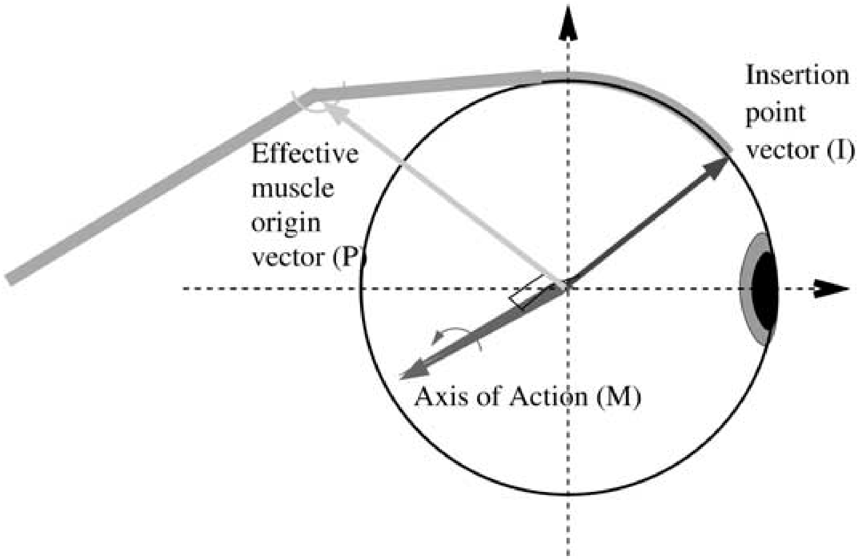

Fig. 1. Determining the axis of action ($\hat{\mathbf{M}}$) of a muscle. The muscle path is constrained at two points, the insertion point **I** on the eyeball and the effective muscle origin at the muscle pulley **P**. The muscle pulls **I** towards **P**. Thus, the eye rotates in the $\vec{\mathbf{I}}$, $\vec{\mathbf{P}}$ plane. The axis of action $\hat{\mathbf{M}}$ around which the muscle causes the eye to rotate is therefore perpendicular to $\vec{\mathbf{I}}$ and $\vec{\mathbf{P}}$.

where $\hat{\mathbf{M}}_i$ is normalized since the axis of action specifies only the direction of torque and not the exerted torque magnitude.

DETERMINING WHETHER $\hat{\mathbf{M}}_i$ CAN BE INDEPENDENT OF EYE ORIENTATION

Since $\vec{\mathbf{I}}_i$ is fixed relative to the eye, $\vec{\mathbf{I}}_i(\vec{\mathbf{R}})$ will depend on eye orientation ($\vec{\mathbf{R}}$). Unfortunately, the location of the muscle pulleys is still uncertain and may change as a function of vergence.[12] Even if we consider $\vec{\mathbf{P}}_i$ to be unknown, however, equation 1 tells us that $\hat{\mathbf{M}}_i \perp \vec{\mathbf{I}}_i(\vec{\mathbf{R}})$, i.e. $\hat{\mathbf{M}}_i$ is in the plane perpendicular to $\vec{\mathbf{I}}_i(\vec{\mathbf{R}})$, which we will refer to as $\mathbf{A}_{\mathrm{I(R)}}$. Thus, $\hat{\mathbf{M}}_{\mathrm{i}}$ is version and vergence independent if:

$$\hat{\mathbf{M}}_i \perp \hat{\mathbf{I}}_i\left(\vec{\mathbf{R}}\right) \forall \vec{\mathbf{R}} \tag{2}$$

Since $\hat{\mathbf{M}}_i \in \mathbf{A}_{\mathrm{I(R)}}$, equation 2 can only be satisfied if

$$\mathbf{A}_{\mathbf{I}(\mathbf{R}_1)} \cap \mathbf{A}_{\mathbf{I}(\mathbf{R}_2)} = \mathbf{A}_{\mathbf{I}(\mathbf{R}_1)} \cap \mathbf{A}_{\mathbf{I}(\mathbf{R}_3)} \forall \vec{\mathbf{R}}_{1,2,3}, \tag{3}$$

where $\vec{\mathbf{R}}_1$, $\vec{\mathbf{R}}_2$ and $\vec{\mathbf{R}}_3$ define three eye orientations with different version and/or vergence.

FINDING THE OCULOMOTOR GEOMETRY THAT WOULD RESULT IN L2

For simplicity, we will focus on vertical version movements and assume that the EOM pairs can be modeled as orthogonal (i.e. at primary position, with zero convergence, a vertical version movement uses only the vertical muscle pair).

If version and vergence are controlled independently, then vertical version movements will actively use only the vertical muscle pair, regardless of the vergence angle. Since only the vertical muscle activity will be changed, the rotation of the eye ($\Delta\vec{\mathbf{R}}$) will be determined by the net change in the torque produced by the vertical muscle pair ($\Delta\vec{\mathbf{T}}_{\mathrm{vert}}$). The requirement to follow L2 therefore determines not only the orientation of $\Delta\vec{\mathbf{R}}$ but also the orientation of $\Delta\vec{\mathbf{T}}_{\mathrm{vert}}$, ($\|\Delta\vec{\mathbf{R}}\| = \|\Delta\vec{\mathbf{T}}_{\mathrm{vert}}\|$).

If we assume strict agonist-antagonist muscle pairing, where every increase in agonist muscle force is accompanied by and equal decrease in antagonist muscle force,[6–10] then

$$\left\|\Delta\vec{\mathbf{T}}\right\| = \frac{\hat{\mathbf{M}}_{\mathrm{ag}} - \hat{\mathbf{M}}_{\mathrm{ant}}}{\left\|\hat{\mathbf{M}}_{\mathrm{ag}} - \hat{\mathbf{M}}_{\mathrm{ant}}\right\|}, \tag{4}$$

where $\hat{\mathbf{M}}_{\mathrm{ag}}$ and $\hat{\mathbf{M}}_{\mathrm{ant}}$ are the axes of action (i.e. the direction of torque) of the agonist and antagonist muscles. The contribution of the antagonist to $\Delta\vec{\mathbf{T}}$ is in the opposite orientation to $\hat{\mathbf{M}}_{\mathrm{ant}}$ (i.e. $-\hat{\mathbf{M}}_{\mathrm{ant}}$ instead of $+\hat{\mathbf{M}}_{\mathrm{ant}}$) because the reduction in antagonist activity causes the net torque produced by all EOMs to shift in the direction opposite to the torque generated by this muscle.

In addition to the requirements set by equation 4, we already know from equation 1 that $\hat{\mathbf{M}}_{\mathrm{ag}} \perp \vec{\mathbf{I}}_{\mathrm{ag}}$ and $\hat{\mathbf{M}}_{\mathrm{ant}} \perp \vec{\mathbf{I}}_{\mathrm{ant}}$. The axes of action that would generate L2 as an epi-phenomenon of independent control of version and vergence can therefore be computed by combining the constraints imposed by equations 1 and 4.

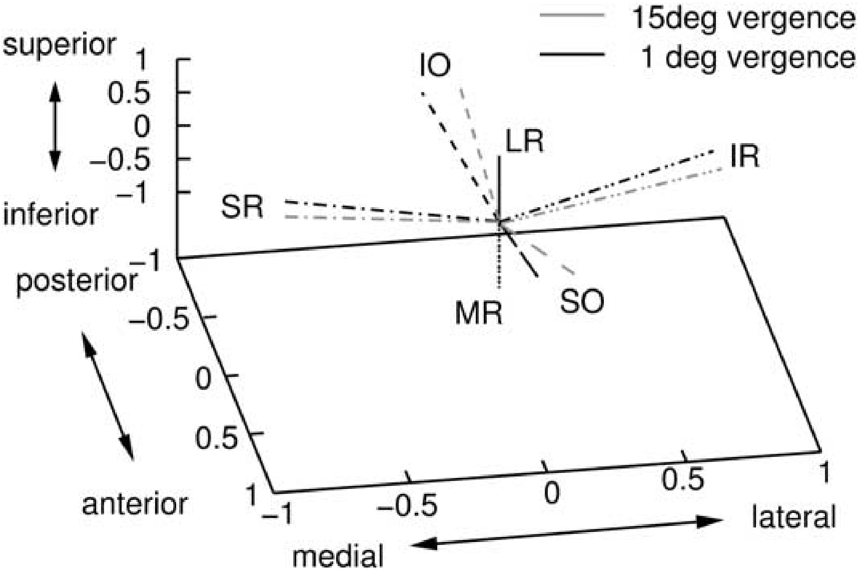

Fig. 2. Axes of action of all six eye muscles of the left eye for 1° vergence, 0° version and 15° vergence, 0° version. Of the plane of possible axes of action per vergence orientation, we show the axes that are closest to the primary position axes of action. For the superior rectus, inferior rectus, superior oblique and inferior oblique muscles, the angle between the axis of action orientation at 1° vergence and at 15° vergence is 7.8°.

Once $\hat{\mathbf{M}}_i$ are determined, the corresponding muscle pulley locations can easily be computed. From equation 1 we know that $\vec{\mathbf{P}}_i \perp \vec{\mathbf{M}}_i$. Thus, all we need to do is determine the plane perpendicular to $\hat{\mathbf{M}}_i$ and disallow those positions that would be clearly unphysiological (i.e. the pulley of the superior rectus should be behind and above the center of rotation and the pulleys of the inferior oblique muscle should be behind and below the center of rotation).

Results

THE AXIS OF ACTION DEPENDS ON VERGENCE ORIENTATION Figure 2 shows the lines of intersection of $\mathbf{A}_{I(R1)} \cap \mathbf{A}_{I(R2)}$ and $\mathbf{A}_{I(R1)} \cap \mathbf{A}_{I(R3)}$ for all six EOMs, where $\mathbf{R}_1 \hat{=}$ (0° vergence, 0° version), $\mathbf{R}_2 \hat{=}$ (1° vergence, 0° version) and $\mathbf{R}_3 \hat{=}$ (15° vergence, 0°version).

For the vertical (SR & IR) and oblique (SO & IO) muscles the angle between the lines of intersection of $\mathbf{A}_{I(R1)} \cap \mathbf{A}_{I(R2)}$ and $\mathbf{A}_{I(R1)} \cap \mathbf{A}_{I(R3)}$ is 7.8°, violating the requirements formulated in equation 3. The orientation of the axes of action of the vertical and oblique muscles therefore changes as a function of vergence, regardless of muscle pulley location. Truly independent control of version and vergence is, therefore, impossible. Figure 3 shows the error in eye orientation that would result if the control of vertical version did not take into account the vergence orientation, assuming the minimum possible axis of action change as a function of vergence.

The scale difference between the plots for the effect on binocular gaze direction and the effect on ocular torsion (Figure 3 top and bottom) clearly shows that vergence primarily affects ocular torsion.

OCULOMOTOR GEOMETRY THAT WOULD RESULT IN L2 Figure 4 shows the range of $\hat{\mathbf{M}}_{SR}$ and $\hat{\mathbf{M}}_{IR}$ that will yield L2 as an epi-phenomenon of independent control of version and vergence (with a gaze direction error <1°).

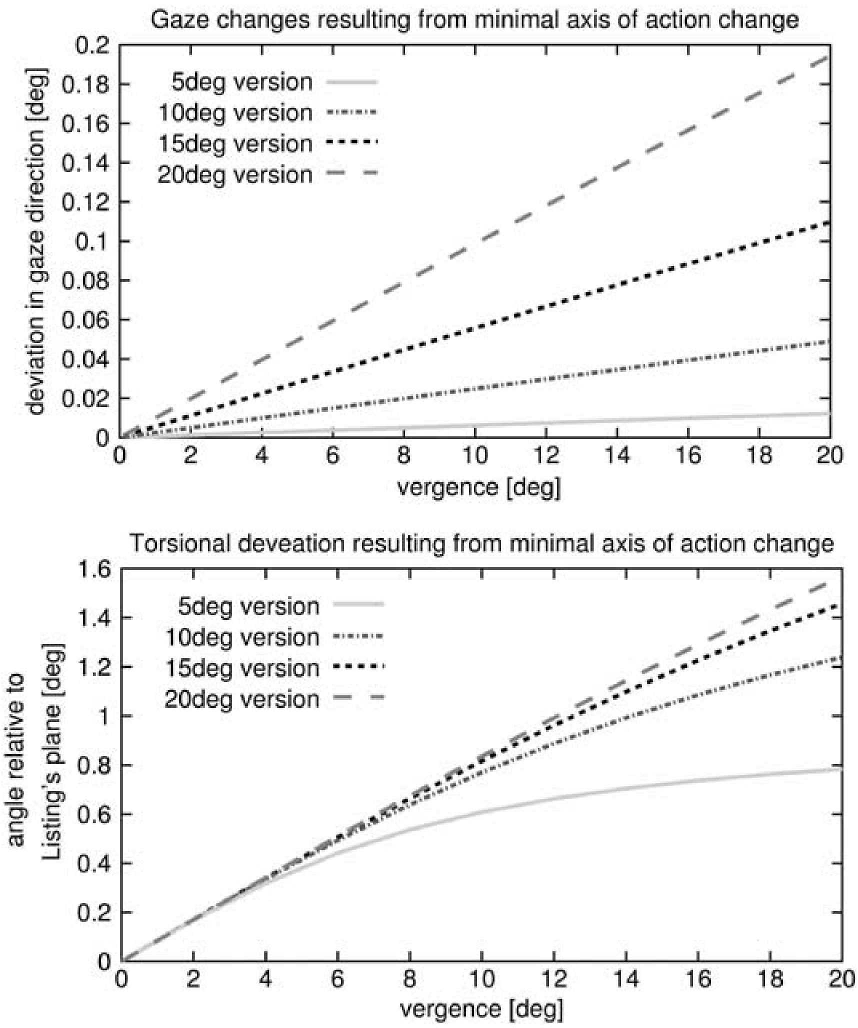

Fig. 3. The top figure shows the change in cyclopean gaze direction and the bottom figure shows the torsional deviation from Listing's plane resulting from the change in axis of action orientation. Both are shown as a function of vergence angle, for different amplitudes of vertical version movements.

Due to the relationship described in equation 4, each of these possible $\hat{\mathbf{M}}_{\text{SR}}$ has one corresponding $\hat{\mathbf{M}}_{\text{IR}}$ that it needs to be paired with.

Using equation 1, each of these possible axes of action yields a plain of possible muscle pulley locations. After disallowing the physiologically impossible pulley positions, the possible muscle pulley positions are found to be in the areas shown in Figure 5.

While there is overlap between the areas of possible pulley positions for the various degrees of vergence, the nature of the coupling between the antagonistic muscles is such that the possible pulley positions for at least one of the two muscles always falls outside this area. Thus, if L2 is an epi-phenomenon of the mechanical interdependence between version and vergence movements, then the muscle pulleys must move as a function of vergence.

Discussion In this study, we used computational modeling of the geometry of the eye plant to show how the vergence orientation of the eye affects the control of version eye movements. For vertical version movements we calculated the muscle pulley locations that would cause

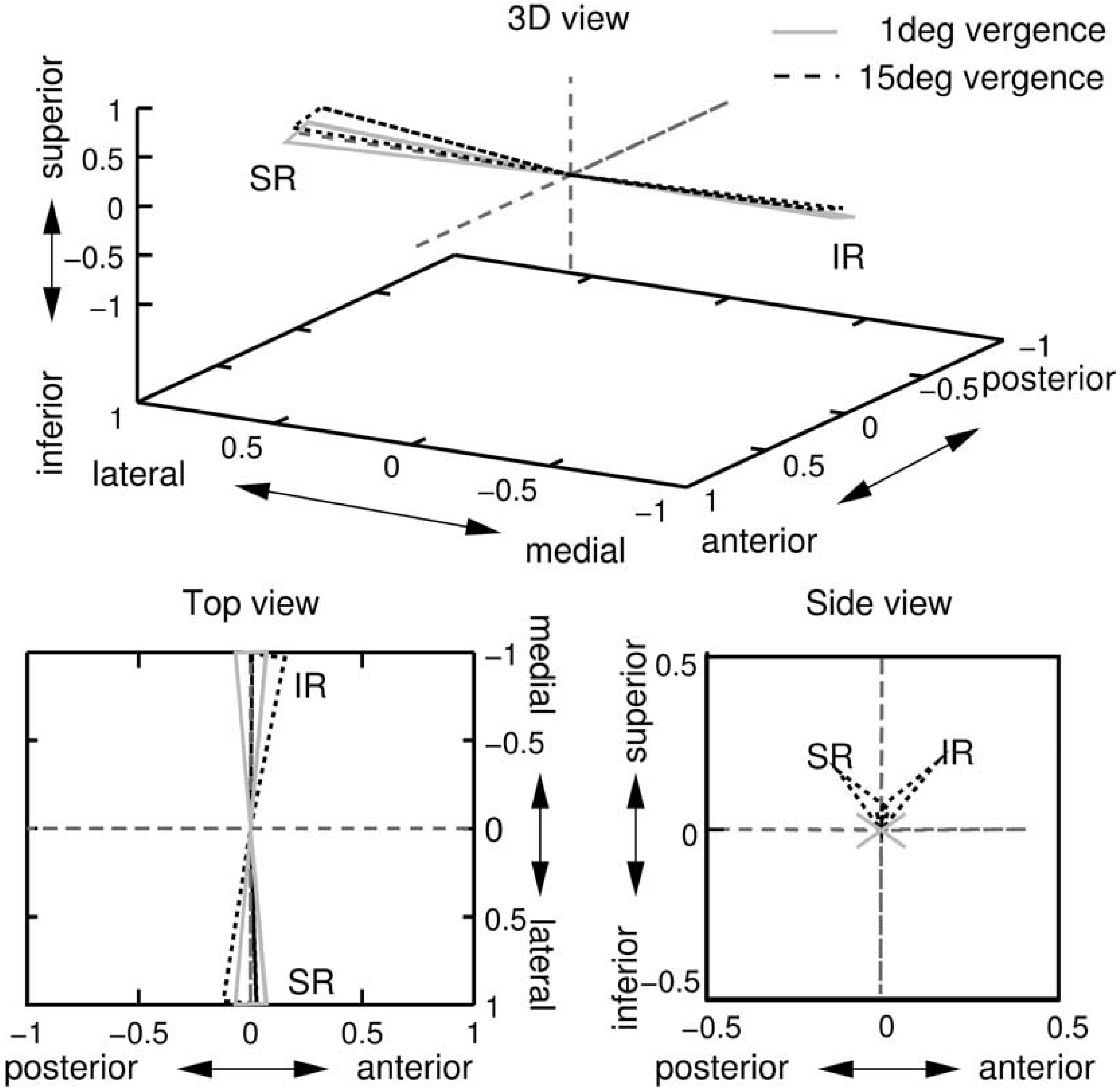

Fig. 4. Possible axes of action of the superior and inferior rectus muscles that generate the binocular extension of Listing's law (L2) as an epiphenomenon of independent control of version and vergence (with gaze direction error <1°). The solid circumference contains the possible axes of action at 1° vergence, the dashed circumference contains the possible axes of action at 15° vergence.

vergence-dependent axis of action shifts to result in the, experimentally found,[3] vergence-dependent tilting of Listing's plane.

This study focused on vertical movements because, assuming orthogonal muscle pairs, for this class of movements the 0° vergence control signal is clearly defined as an activity change in only the vertical EOMs. A requirement to change the activity in any of the other EOMs is therefore easily detected as a vergence-dependent change in the eye movement control signal. In principle, the same methodology we used here can also be applied to horizontal and diagonal eye movements.

In this study, we provided a link between the work that has recently been done concerning the mechanics of the eye plant and the models

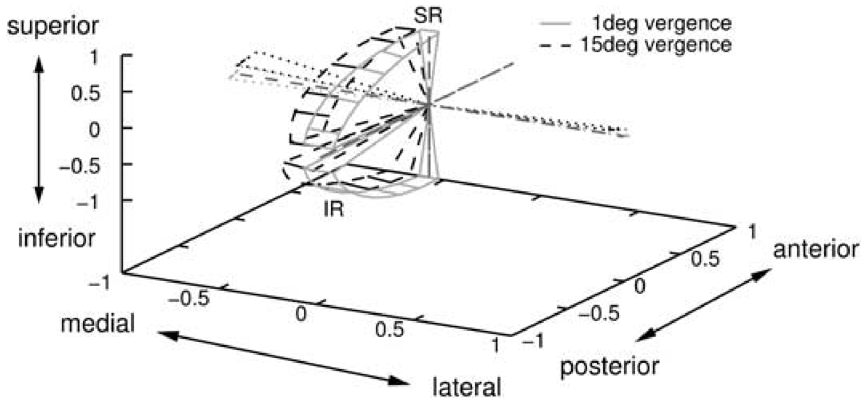

Fig. 5. Possible pulley positions of the SR and IR muscles that yield L2 as an epi-phenomenon of independent control of version and vergence (with gaze direction error <1°). The solid circumference contains the possible pulley positions at 1° vergence, the dashed circumference contains the possible pulley positions at 15° vergence.

of binocular control of eye movements. Here we have shown under what conditions (which muscle pulley positions) the cyclotorsion following ocular convergence, described by the binocular extension of Listing's law,[3] could arise as an epi-phenomenon of the mechanics of the eye plant.

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