Misrepresentations and Confusion in the Oculomotor Plant

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The debate surrounding the implementation of Listing's law and the half-angle rule has become heated over the last decade with strong support on different fronts. One issue of contention surrounds the function of the oculomotor pulleys themselves and whether or not they are innervated in such a way to implement the half-angle rule. Support for pulley innervation has largely stemmed from magnetic resonance imaging studies that demonstrate how pulleys alter their orientation with different eye positions and how certain eye muscle fibers terminate, and perhaps innervate, the pulleys themselves.[1,2] In contrast, others have found that destruction of the lateral rectus pulley does not affect the amplitude or velocity profiles of stimulation-induced eye movements, indicating no role for the pulleys.[3] Thus, the debate over pulley innervation persists without a solution.

Another issue of dispute surrounds the neural versus mechanical realization of the half-angle rule. On one side, proponents support a neural basis of implementation in which the brain determines ocular torsion and sends these commands to the eye via the nuclei and nerves that control it (cranial nerves III, IV and VI). The other side favors a mechanical implementation in which the ocular pulleys that surround and guide the eye change their orientation with changes in eye position. Part of the reason that this debate has become so contentious is that three-dimensional ocular kinematics and the mathematics that are inherent to rotating objects such as the eye are extremely complex to grasp, even to many close to the field. Our lab set out to investigate what the brain tells eye muscles to do by recording from cyclovertical[4] and stimulating horizontal[5] oculomotoneurons.

It was to our dismay that we read the paper by Lee, Lai, Brodale and Jampolsky entitled "Sideslip of the medial rectus muscle during vertical eye rotation,"[6] especially concerning their erroneous summary and critique of our recent work. While misquoting our papers,[4,5] the authors state that "if one wants to find out how Listing's law or, equivalently, the half-angle rule is implemented in horizontal eye movements…the abducens neurons and the lateral rectus muscle are the last place to look because implementing the law for horizontal eye movements requires changing the rotation axis vertically; for this, the lateral rectus muscle is an insignificant player." This statement both misrepresents what our experiments were about and partially misguides what should be done.

First, we agree that single-unit recording from horizontal motoneurons like those in the abducens nuclei would not yield fruitful results since changes in motoneuron firing should be observed in the nuclei that control torsion (i.e., the vertical eye muscles). But

even a simple scan through the Ghasia and Angelaki paper[4] would indicate that we did indeed record from the vertical motorneurons (i.e., oculomotor and trochlear nerves and nuclei) and not the horizontal motoneurons as Lee et al. mistakenly claim.

Second, we assert that stimulating the nuclei/nerves that innervate the horizontal muscles is precisely what should be done in order to determine if three-dimensional kinematics are implemented neurally or mechanically. The fact that Klier et al.[5] found that the half-angle rule was still implemented when the horizontal system was activated, while the normal neural pathways for cyclovertical rotations were bypassed, most convincingly indicates a mechanical implementation of Listing's law. The only way in which a half-angle rule could emerge in our electrical stimulation experiment is if the plant implemented it itself. Stimulation of the cyclovertical motoneurons and nerves is precisely the incorrect approach since one can no longer distinguish between neural or mechanical factors when stimulation evokes vertical and torsional eye movements simultaneously.

The complexities of ocular anatomy and physiology are indeed difficult to grasp; however, their understanding is key to helping those with strabismus and other eye muscle-related deficits. Unfortunately, this goal is only made more difficult by blatant misquotes and the condemnations of correct experiments. In the last several years there has been great stride in uniting the two disparate views and recognizing that both neural and mechanical factors play important roles in three- dimensional kinematics. This progress should not be undone.

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