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Motor Control: Three-Dimensional Metric of Head Movements in the Mouse Brain

Arseny Finkelstein
Janelia Research Campus, Howard Hughes Medical Institute, Ashburn, Virginia 20147, USA
Correspondence: arsenyf@gmail.com

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Many forms of human and animal behavior involve head movements. A new study reveals the neural code for three-dimensional head movements in the midbrain of freely moving mice.

As I am typing these words, my head and eyes are constantly moving in different directions to follow the letters on the monitor. Occasionally, I am turning my head down to look at the keyboard or sideways to prepare a reach towards my coffee mug. In fact, most of our interactions with the world involve orienting movements towards different points of interest in three-dimensional space. Orienting behaviors are crucial for all animals in multiple contexts, such as exploration or in response to attractive or aversive stimuli. However, little is known about how three-dimensional orienting movements are encoded in the brain of freely moving animals. An important step has now been made by Wilson *et al.* [1], who report in this issue of *Current Biology* their new study of the neural representation of three-dimensional head movements in freely moving mice.

In 1870, Adamuk [2] reported that electrical stimulation of the superior colliculus induces eye movements. Research conducted a century later, primarily in head-fixed monkeys, revealed that neurons in this brain region encode a metric for fast eye movements called saccades. Specifically, neurons in the deep subdivision of the superior colliculus were shown to respond preferentially to a particular saccade vector — defined by direction and size of the resulting eye displacement, irrespective of the initial eye position [3]. These neurons produced a vigorous burst of activity shortly before eye-movement initiation. Microstimulations of different parts of the superior colliculus resulted in saccade vectors that varied systematically according to the site of stimulation [4]. Furthermore, neurons recorded at corresponding locations during natural eye movements showed preferences to saccade vectors matching those evoked by microstimulations [5], indicating that this brain region contains a topographic map of eye movements.

In addition to eye movements, in a variety of species, microstimulation of the superior colliculus has been shown also to induce movements of the head and other body parts [6]. These observations suggest a role of the superior colliculus in orienting movements in general. In primates, orienting responses typically involve combined eye and head movements [7], aimed at centering points of interest in space on the fovea — the part of the retina that has the highest visual resolution. In contrast, animals without foveae, such as rodents, do not make saccades and likely rely on rapid head movements for orienting behaviors. Inactivation of the superior colliculus affects the performance of rats in decision-making tasks that require spatial orienting [8,9], and neurons in the superior colliculus recorded during these tasks were shown to encode choice direction [8]. Before the study by Wilson *et al.* [1], however, the metric and the dimensionality of head-motion repertoire encoded in the rodent superior colliculus were unknown, partially because of the difficulty in tracking three-dimensional head movements.

To study three-dimensional head movements in freely moving mice, Wilson *et al.* [1] developed an inertial-sensor-based system for tracking the three Euler angles of head rotation: yaw, pitch, and roll (Figure 1A), while recording single neuron activity in the superior colliculus. In this experiment, mice foraged inside a behavioral arena and exhibited extensive three-dimensional head rotations. Wilson *et al.* [1] found that about 10% of the recorded neurons showed consistent preferences to head movements of a certain amplitude and direction in yaw, pitch, or roll. Individual neurons were tuned to head movements in one, two, or three angular dimensions, with the majority of motion-tuned neurons encoding rotations in yaw or pitch. Each neuron produced a burst of activity for a particular head-displacement angle. These bursts occurred shortly before or during the early stages of head movement (Figure 1B), analogously to bursting activity of neurons in the monkey superior colliculus prior to saccadic eye movements [3]. Interestingly, the angular preference of head-motion-tuned neurons did not depend on the firing rate within a burst or on the burst duration. Instead, firing rates of more than half of these cells were highly correlated with head angular velocity (Figure 1C), in one or more Eulerian components of head rotation. Taken together, these findings suggest that motion-tuned neurons in the mouse superior colliculus not only represent the metric of three-dimensional head movements, but also encode certain aspects of movement kinematics.

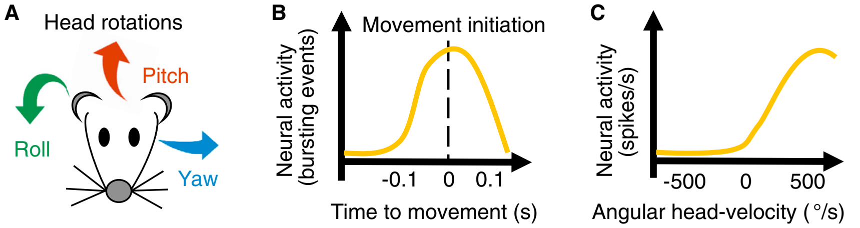

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Figure 1. Schematics of motion tuning to three-dimensional head movements in the mouse superior colliculus.
(A) The three Euler angles of head rotation (yaw, pitch, and roll). (B) Neurons responded by bursts of activity around the time or shortly before the initiation of preferred head movements. Each neuron responded by bursts of activity to head movements within a certain range of displacements in yaw, pitch, or roll. (C) Firing rates of many neurons were modulated by angular velocity of the head in yaw, pitch, or roll.

For successful navigation in space, head movement representation should be transformed from a body-centered (egocentric) to a world-centered (allocentric) reference frame. Tracking head-direction in allocentric reference frame is carried out by head-direction cells that discharge selectively whenever the head is pointing at the preferred direction of a neuron in allocentric space, analogously to a compass [10]. Head-direction cells with three-dimensional allocentric tuning have been found in the dorsal presubiculum of bats [11], and were recently reported in the anterior dorsal thalamus of mice [12]. Wilson *et al.* [1] analysed the existence of allocentric tuning in the superior colliculus and found that the vast majority of recorded neurons, including motion-tuned neurons, were not modulated by allocentric head direction. Furthermore, Wilson *et al.* [1] reported only minor changes in the tuning of most head-motion cells in darkness, indicating little contribution of visual landmarks or optic flow to the motor tuning of these neurons. These results suggest that integration of allocentric and egocentric coding of head-motion might occur outside of the superior colliculus, perhaps in parietal or retrosplenial cortices where neurons with both allocentric and egocentric tuning have been found [13,14].

Previous studies in primates have suggested that the roll component of eye-head movements is represented downstream of the superior colliculus [15], implying that the motor map in this brain region is two-dimensional. This conclusion was based on comparison of eye and head movements during normal behavior and microstimulation experiments. In contrast, Wilson *et al.* [1] found motor tuning to all three Euler angles of head rotation, suggesting a three-dimensional representation of head motion in the mouse superior colliculus. However, out of the three Euler angles of head motion, roll was least represented, which might partially explain the seemingly two-dimensional motor representations in primates. Interestingly, roll was also least represented by three-dimensional head-direction cells in bats [11]. The absence of strong roll representation by head-motion and head-direction cells across species might relate to the fact that roll does not define the heading direction in three-dimensional space, and thus might be less ethologically relevant for orienting behavior and navigation [16]. Notably, recent recordings in the superior colliculus of echolocating bats revealed neurons tuned to object position in egocentric three-dimensional space [17]. The distance tuning of these neurons became shorter when bats actively inspected objects in the environment, suggesting that multi-dimensional neural representations in the superior colliculus could be modulated dynamically according to the behavioral needs of the animal.

Rodents can move their eyes, but eye movements become much smaller in amplitude in the absence of large head movements [18]. Future neural recordings with combined eye and head tracking would be needed to understand if eye movements contribute to the head-motion tuning in the mouse superior colliculus. Notably, microstimulation of the rat superior colliculus resulted in contralateral eye movements that were organized according to a topographic map [19], suggesting commonalities in the organizational principles of motor maps in the superior colliculus across species. Many neurons in the study by Wilson *et al.* [1] showed a preference to downward pitch and were tuned to relatively small head displacements. This might indicate that the recording locations in this experiment only partially sampled the putative motor map, in case such a map exists in the mouse superior colliculus. Systematic manipulations and recordings of neural activity would provide a more comprehensive understanding of the organizational principles of three-dimensional representations of head movements in the mouse superior colliculus.

The superior colliculus is part of a larger network of brain regions involved in orienting behaviors and movement planning [20]. Future work would be needed to address whether motion-tuned neurons in the superior colliculus revealed by Wilson *et al.* [1] play a causal role in the initiation and control of three-dimensional head movements, and how their activity is related to the function of other nodes in the network. The discovery of a neural representation of head movements in the mouse by Wilson *et al.* [1] further suggests that motor codes in the superior colliculus are largely conserved across species, and makes an important contribution to the effort of understanding the neural mechanisms of orienting behaviors in a genetically accessible model organism.

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Neural Circuits: When Neurons 'Remember' Their Connectivity

Margaret L. Veruki[1] **and Timm Schubert**[2,*]
[1]Department of Biomedicine, University of Bergen, 5009 Bergen, Norway
[2]Centre for Integrative Neuroscience (CIN) and Institute for Ophthalmic Research, University of Tübingen, 72076 Tübingen, Germany
*Correspondence: timm.schubert@cin.uni-tuebingen.de
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Loss of neurons due to injury or neurodegeneration can lead to dramatically altered neural circuits, resulting in reduced or lost function. One mechanism to preserve function could be to re-establish the stereotypic connectivity among the remnant neurons. In the mammalian retina, such a selective re-wiring has now been described.

In the central nervous system, neural connectivity determines function. When the architecture of specific neural circuits is damaged by the loss of neurons, either due to a one-time event such as a stroke or brain injury, or due to hereditary diseases such as retinitis pigmentosa, the loss of function can be devastating. It is of crucial importance to understand how these changes in neural architecture affect the functional state of the network and whether endemic mechanisms can be exploited to restore function. During degenerative events in the mammalian central nervous system, damaged neurons do not regenerate,