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## The Middle Temporal Area Does Not Relay Vestibular Signals

Alexis D. J. Makin,<sup>1</sup> Kelly Wild,<sup>2</sup> and Rochelle Ackerley<sup>2</sup>

<sup>1</sup>School of Psychological Science and <sup>2</sup>Faculty of Life Sciences, University of Manchester, Manchester M60 1QD, United Kingdom  
Review of Chowdhury et al.

The primate brain middle temporal (MT) and medial superior temporal (MST) areas have an intriguing relationship. It is conventionally thought that MT neurons respond to retinal motion stimuli (Born and Bradley, 2005), whereas MST cells respond both to retinal and extraretinal inputs (Assad and Maunsell, 1995). Area MST can be divided into two functionally distinct parts, namely the dorsal subdivision (MSTd) and the lateral subdivision. Both subdivisions are sensitive to visual motion signals and both receive vestibular input. Neurons in MSTd respond to self-motion, such as rotation, even in the absence of significant visual input (Takahashi et al., 2007). The integration of visual and vestibular information by MSTd is essential for real-world navigation, in which the interplay between object motion, optic flow, and self-motion can produce potentially ambiguous signals (Warren and Rushton, 2009).

It is known that MSTd receives visual motion information from area MT (Born and Bradley, 2005); however, the pathway from the vestibular nuclei to MSTd is unknown. In a recent paper, Chowdhury et al. (2009) raised a simple question: is the

vestibular input to MSTd relayed via MT (along with visual signals)? Although MT is not usually thought to process extraretinal motion signals, a recent article by Nadler et al. (2008) suggested that extraretinal inputs to MT may help encode depth from motion parallax. In light of this, Chowdhury et al. (2009) interrogated a population of MT neurons with microelectrode recording techniques in an attempt to determine whether vestibular signals exist in MT. A previous study used a similar experimental setup to investigate vestibular tuning in MSTd (Takahashi et al., 2007).

Single-unit neuronal activity was recorded from MT and MSTd in three rhesus monkeys. Visual stimuli were projected onto a screen in front of the monkey, which was secured in a chair. The experiment had two main conditions: (1) a “visual” condition in which dots moved to simulate self-rotation or self-translation through a cloud of dots while the monkeys were static, and (2) a “vestibular” condition in which the monkey was subjected to rotational or translational motion while fixating a central spot that was head fixed.

A “direction discrimination index” (DDI), indicating that the directional selectivity of a neuron, was computed for each recorded neuron. Responses from 55 MT neurons were recorded in both vestibular and visual rotation conditions. All MT neurons showed significant visual direction tuning, and, moreover, half showed significant vestibular tuning. In

these rotational conditions, the DDI was greater in the visual than the vestibular condition. In the translation condition, all 47 recorded cells showed visual tuning, but only 17% showed vestibular tuning. This initial result suggested that vestibular signals were present in area MT.

However, subsequent analysis of the vestibular conditions proved this conclusion to be premature. Despite the fact that the monkeys were trained to suppress their vestibulo-ocular reflex (VOR) during the vestibular conditions, incomplete suppression of the VOR could produce retinal slip of the visible features such as the fixation cross, screen edge, or dim background texture. Consequently, apparent vestibular tuning could have been produced by visual motion signals resulting from retinal slip. This alternative explanation was supported by several lines of evidence. First, the neurons that responded to a particular direction of visual movement often responded primarily to self-rotation in the opposite direction. In such a vestibular condition, incomplete VOR suppression would produce retinal slip in the preferred visual motion direction of the neuron. Second, analysis of eye movements during the vestibular conditions showed that the effect of the VOR was not completely suppressed. Third, the alternative account predicted that incomplete VOR suppression would produce greater excitation of MT neurons that are sensitive to motion near the visible fixation cross, and this prediction was confirmed. Finally, the vestibular rotation

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Correspondence should be addressed to Rochelle Ackerley, Faculty of Life Sciences, University of Manchester, Moffat Building, Sackville Street, P.O. Box 88, Manchester M60 1QD, UK. E-mail: rochelle.ackerley@manchester.ac.uk.

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condition was repeated in absolute darkness, with no visual input, and this abolished the apparent vestibular tuning in area MT.

MSTd neurons were also recorded during the vestibular rotation condition. Unlike the MT cells, the MSTd cells showed genuine vestibular tuning, even in total darkness. However, the strength of this response was smaller than that found in a previous study by Takahashi et al. (2007). This difference could have arisen because the previous investigation was not conducted in total darkness. Therefore, retinal slip resulting from incomplete VOR suppression may have accounted for a proportion of the apparent MSTd vestibular tuning in that study. A significant contribution of the current study is the confirmation that the vestibular tuning in MSTd is not entirely attributable to incomplete VOR suppression (unlike apparent vestibular signals in MT).

Of the millions of neurons in area MT, Chowdhury et al. (2009) only sampled a very small proportion and found no vestibular tuning. Based on this null result, they concluded that area MT does not send vestibular signals to area MSTd, and thus the significant vestibular tuning in MSTd must arise from other, as yet unknown, pathways. Chowdhury et al. (2009) did not explicitly address the problems inherent in interpreting a null result. It is akin to sampling a very small proportion of people at a sports event and, on finding out that none of them are neuroscientists, generalizing that neuroscientists do not go to sport events. Their conclusion, however, remains plausible. One supporting argument the authors could have given is that genuine vestibular tuning in MSTd was clearly evident despite the fact that a

very small proportion of MSTd cells were sampled. The difference in responses between MT and MSTd is unlikely to occur by chance if vestibular tuning in the areas were equivalent.

Making the assumption that MT does not relay vestibular signals to MSTd, these authors suggest other putative pathways. One possibility they discuss is that signals from the cerebellar vermis may be relayed to MSTd. This is supported by the finding that the cerebellar vermis, like MSTd, discriminates between head tilt and head translation. It is likely that future experiments will identify the unknown pathway of vestibular input to MSTd. Lesions to the cerebellar vermis, for example, may abolish vestibular tuning in MSTd, in the same way as surgical removal of the vestibular labyrinth did in a previous investigation (Takahashi et al., 2007).

Nadler et al. (2008) recently explored the role of extraretinal inputs to MT in relation to depth perception. When a point is fixated in space, a translational movement of the observer makes objects that are farther away than the fixation point move across the retina in the same direction as the observer, and objects closer than the fixation point move in the opposite direction to the observer. This motion parallax is an indicator of the relative depth of different objects but only if extraretinal cues provide the crucial information about the direction of observer translation. Nadler et al. (2008) found that, when extraretinal cues indicating self-motion were present, some MT neurons responded preferentially to a particular combination of visible and observer motion. These neurons were thus able to discriminate relative depth. In a follow-up paper, it was found that efference copy of

the motor smooth pursuit command, rather than vestibular signals, were the crucial source of extraretinal information in MT (Nadler et al., 2009). The results of Nadler et al. are consistent with those from Chowdhury et al. (2009) because they both suggest that vestibular information is not coded in area MT. It can be concluded from these studies that area MST encodes a world-centered representation of object motion by integrating MT inputs with vestibular signals that originate from a different, and currently unidentified, neural pathway.

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