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Neural encoding of proprioception of the limbs in the mouse primary somatosensory and motor cortices

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Rodents rely on proprioceptive information from the periphery to guide and coordinate precise forelimb and hindlimb movements, a process called sensorimotor integration. The mouse primary somatosensory (S1) and primary motor (M1) cortices are known to be necessary for adapting motor commands to new sensory environments, and recent work suggests neurons in the forelimb area of S1 encode proprioceptive information about contralateral forelimb movement. However, we do not know how proprioception of all four limbs is represented across multiple brain regions. To address this question and to isolate pure somatosensory responses (proprioception and touch) from motor commands that would be present in awake animals, we recorded neural responses to passive movement of ipsilateral and contralateral limbs in eight mice under anesthesia. Using stereotaxic coordinates to locate S1 and M1 forelimb and hindlimb areas, we performed unilateral two-photon imaging over these two regions simultaneously in mice expressing GCaMP6s, a highly sensitive fluorescent indicator of neuronal activity. A brushing motion was used to provide cutaneous and proprioceptive stimulation to each limb (blocks of five trials per limb were repeated across three cycles). Altogether, we recorded the activity of 12,895 neurons, of which 2,053 neurons (16%) were significantly modulated by passive movement of at least one limb ($p < 0.02$, Wilcoxon rank-sum test on single trial responses vs. baseline). Of significantly modulated neurons, 48% responded to movement of the contralateral hindlimb, 15% to the ipsilateral hindlimb, 30% to the contralateral forelimb, and 7% to the ipsilateral forelimb. A subset of neurons (9%) was significantly modulated by more than one type of limb movement, most often ipsilateral and contralateral hindlimb movement. In terms of response amplitude, neurons that were significantly modulated by contralateral movements had larger responses than those modulated by ipsilateral movements (hindlimb: $dF = 0.90 \pm 0.01$ SEM contralateral vs. $dF = 0.79 \pm 0.01$ SEM ipsilateral, p = 5.1 x 10-39; forelimb: $dF = 0.78 \pm 0.01$ SEM contralateral vs. $dF = 0.74 \pm 0.01$ SEM ipsilateral, $p = 0.012$). In summary, we found evidence of proprioceptive signals related to both ipsilateral and contralateral forelimbs and hindlimbs across primary somatosensory and motor cortices of the mouse. The distributed nature of these responses, across cortical regions and limbs, could be an indication of how proprioception guides the formation of motor commands within the mouse cortex.

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