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Heterogeneous reference frames for reaching in macaque PMd

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Visually-guided reaching necessitates a transformation from retinal coordinates to commands to the musculature. We investigated the reference frames used to plan reaches in the dorsal premotor cortex (PMd). Recordings were made with 4x4mm chronic arrays implanted in the caudal aspect of PMd of two macaques. Monkeys performed a delayed reach task, moving from a set of initial eye and hand positions to ten targets. Initial eye and hand positions were designed so that target locations could be varied independently in either eye-centered or limb-centered coordinates. We performed two analyses. First, we tested whether changing the retinal and/or limb-centered position of the target modulated the neural response. Second, we tested whether neurons'response fields were more tightly linked to the eyes or to thehand.

Of 147 neurons recorded in two monkeys, 98 were tuned for the reach target during the delay period, 74 were significantly influenced by the retinal position of the target, and 93 were influenced by the limb-centered position of the target (ANOVA, $p<0.05$). Thus, the retinal location of the reach goal influences half of PMd neurons, and exerts nearly as great an influence in the population as does the limb-centered location of the goal.

In the reference frame analysis, we found that 31% of neurons have response fields that are more tightly aligned to the eyes than to the limb, while the remaining 69% were more limb-centered than eye-centered. We employed a bootstrap test to establish our confidence in ascribing a particular reference frame to each neuron. We found that for only 53% of neurons could a particular reference frame be assigned definitively. Thus, nearly half of PMd neurons employ a mixed eye-centered and limb-centered reference frame.

We asked if the reference frame of a neuron was consistently associated with any of its other properties. For example, neurons differ in temporal profile, with some cells most active after target appearance, and others active during the reach. No consistent relationship was observed between the timing of a neuron's response and its reference frame. Neurons also differ in the source (eye or hand position) and degree of postural modulation. We could not reliably predict a neuron's reference frame from the postural signals it exhibited. Thus, we found no evidence for distinct subpopulations within PMd. In addition, the reference frames used by PMd neurons did not appear to evolve over the course of the delay period.

Three main conclusions are drawn. First, the retinal location of the reach goal influences half of PMd neurons. Second, these retinal influences combine with limb-centered coding of the reach plan such that an unambiguous eye-centered or limb-centered reference frame cannot be assigned for nearly half of the cells. Third, PMd appears to constitute one mixed population of neurons, and not distinct, interdigitated populations of neurons.

Since PMd does not contain a clear limb-centered representation of the reach goal, either downstream areas must do so, or perhaps a complete transformation away from retinal influences is not necessary for accurate reaching.

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