

## Motion processing in macaque V4

### To the Editor:

A recent study by Tolias *et al.*<sup>1</sup> demonstrated convincingly that neurons in visual area V4 can acquire direction selectivity after adaptation to coherent motion. This is a valuable result because it bears on the role of V4 in motion processing and may also reconcile an apparent discrepancy between neurophysiology and functional imaging of V4 (ref. 2). Moreover, it underscores how dynamic aspects of all types of selectivity can be missed without specific tests. However, the premise of the study, that V4 neurons “are generally not selective for direction of motion”, is not entirely accurate. At least three reports have assessed direction selectivity in V4 quantitatively<sup>3–5</sup> and have found that roughly one-third of V4 neurons are direction selective (preferred:null response ratio  $\geq 2.0$  or  $d\text{-prime} \geq 1.0$ ). A direct comparison<sup>5</sup> between V4, MT and area 7a in the same animals and using coherent random dot stimuli showed that MT neurons had a mean preferred:null ratio of 6.4, compared with 1.8 for V4 and 1.7 for area 7a. Thus, although direction selectivity in V4 is not nearly as pronounced as in MT, it is comparable to other areas in the dorsal pathway. One must also consider that in the macaque, V4 is many times larger than MT<sup>6</sup> and may therefore contain a comparable number of highly direction-selective neurons even if the density of such neurons is much lower. Although the existence of conventional direction selectivity in V4 does not alter the authors’ conclusions about the role of adaptation in stimulus selectivity, we feel that V4 should not be overlooked as a potentially reliable source of conventional

motion signals outside of areas traditionally associated with motion processing.

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### Tolias *et al.* reply:

We agree with Ferrera and Maunsell that V4 could potentially serve as a source of conventional motion signals. This is also supported by our own study<sup>1</sup>, in which we found that 15% of V4 neurons were directionally selective before adaptation (Rayleigh test for circular statistics). The difference between our estimate of the percentage of direction-selective neurons and the estimate of Ferrera *et al.*<sup>2</sup> (they report around 33% direction-selective neurons) probably has a methodological origin. First, the random dot stimulus we used to test direction of motion selectivity had 60% coherence, as opposed to

the 95–99.8% coherent stimulus used by Ferrera *et al.*<sup>2</sup>. Second, as we simultaneously recorded from many neurons, we did not optimize the stimulus parameters (aperture size, dot size and density and speed) individually for each cell. Third, we used different tests and thresholds for statistical significance. In addition, Desimone and Schein<sup>3</sup>, who used moving gratings and a stricter tuning index threshold ( $<0.3$ , response to null/preferred direction) than did Ferrera *et al.*, reported 13% of V4 neurons to be direction-selective, in close agreement with our result. These reasons are likely to account for the difference in estimates of direction selective neurons. It is clear, however, that there is a significant number of V4 neurons (13–33%, depending on estimates) that are tuned to direction of motion even before adaptation. We therefore believe that Ferrera and Maunsell are correct in suggesting that area V4 can be a significant source of conventional motion signals before adaptation. Our paper shows that this role seems to be significantly enhanced after adaptation<sup>1</sup>.

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