# Cortical responses to visual motion in alert and anesthetized monkeys



To the editor—Cortical area MT of macaque monkeys contains direction-selective neurons. Some respond only to the components of complex moving patterns, whereas others compute true pattern motion[1,2]. In *Nature*, Pack *et al.*[3] reported that most MT neurons compute pattern motion in alert macaques but signal only component motion under anesthesia, but we have found the prevalence of component- and pattern-selective neurons to be unaffected by anesthesia[1,2,4]. Pack *et al.* conclude that motion integration circuits are impaired by anesthesia[3]. We believe their results can be explained by their choice of stimuli and anesthetic.

A neuron is classified as component-selective if its responses to 'plaid' patterns (**Fig. 1c**) are proportional to the sum of its responses to the plaids' components[1] (**Fig. 1a** and **b**). However, the plaids used by Pack *et al.*[3] (**Fig. 1d**) are not the sum of the components they used. Where the gratings' bars intersect, the luminance of an additive plaid is doubled, but their stimulus had uniform luminance. A third component (**Fig. 1e**) must be subtracted from the gratings to create their non-additive plaid. Classification using these stimuli requires that the components of the plaid move in a different direction than the plaid itself, but this third component moves in the same direction[5] (**Fig. 1e**). The third component would elicit pattern-like responses from all MT cells, and thus component-selective cells tested with this non-additive plaid would masquerade as pattern-selective. It is therefore inappropriate to use non-additive plaids for this classification method, and the use of these patterns led Pack *et al.* erroneously to claim that most MT neurons in alert animals are pattern-selective.

Why might anesthesia change pattern-like into component-like responses? The third component is low in contrast compared to the grating components. Neurons in MT are very sensitive[6], so such a low-contrast stimulus component would normally be effective. However, Pack *et al.* used isoflurane anesthesia, which substantially reduces contrast sensitivity in cortical and thalamic neurons while only modestly reducing responses to high-contrast stimuli[7,8]. Isoflurane also potentiates GABA-mediated inhibition[9], and thus strengthens the cross-orientation suppression characteristic of cortical responses[10]. These factors would selectively weaken responses to the third component (**Fig. 1e**). Thus, isoflurane would effectively convert non-additive plaids into additive plaids by selectively attenuating the third component. This is relevant only because Pack *et al.* used non-additive plaids; classification using standard additive plaids[1] is unaffected by anesthesia.

We therefore suggest that the findings of Pack *et al.*[3] do not reflect any fundamental property of cortical motion detection, but result instead from unfortunate choices of stimulus and anesthetic. The stimulus led Pack *et al.* to misclassify their neurons in alert animals, and the anesthetic caused this classification to change. These factors explain the apparent difference between their results[3] and ours[1,2,4].

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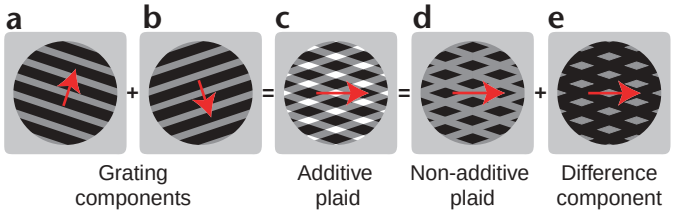


**Fig. 1.** Additive and non-additive plaids. (**a**, **b**) Grating components of (**c**), an additive plaid. (**d**) The non-additive plaid used by Pack *et al.*[3]. (**e**) The component subtracted from (**c**) to create (**d**).

Reply—Movshon *et al.* suggest that we found more pattern cells in alert monkeys because a "third component" in our stimuli "would elicit pattern-like responses from all MT cells." Although this explanation sounds plausible, it has been tested directly and found to be wrong. Stoner and Albright[4] compared, for single MT neurons in alert monkeys, the responses to plaid stimuli with and without the third component. They found that introducing the third component caused MT responses to become less pattern-like and more component-like (Fig. 3b in ref. 4). Moreover, Stoner and Albright's third component was greater in amplitude than ours, so the explanation of Movshon *et al.* cannot be right.

The processing of plaid stimuli is particularly sensitive to small stimulus manipulations[4,5,11], and MT neurons are sensitive to a wide variety of visual cues[12,13]. Consequently, there is no reason to assume that the luminance of the grating intersections accounts for the different results in the different laboratories. The stimuli were not equated for background luminance, retinal eccentricity, stimulus size, grating angle, duty cycle, spatial frequency or contrast, and each of these parameters can strongly influence the processing of plaids[5,11]. At present, we simply do not know which of the stimulus differences is responsible for the different results, and neither do Movshon *et al.* It is precisely for this reason that we held all of these parameters constant in our comparison of the alert and anesthetized states.

The claims about isoflurane and contrast sensitivity from Movshon *et al.* are misleading. In both of the studies cited, the differential effects of isoflurane were confined to temporal frequencies (1 Hz or less) much lower than those used in our study. For the range of frequencies we used (5–10 Hz), the contrast sensitivity found with isoflurane was similar to that

of other anesthetics[8]. Furthermore, both studies are ultimately of questionable relevance to the present issue. One study used a combination of anesthetics that did not include isoflurane[7], and the other involved only parvocellular neurons[8], which have low contrast sensitivity and do not influence the responses of MT neurons appreciably[14].

We wish to emphasize, as we did in our original paper, that there are many candidate models of motion integration in MT, most of which suggest mechanistic interpretations of our experimental results. More importantly, these models make clear predictions, which await the results of further experimentation.

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1. Movshon, J.A., Adelson, E.H., Gizzi, M.S. & Newsome, W.T. *Pontificiae Academiae Scientiarum Scripta Varia* **54**, 117–151 (1985) [also in *Exp. Brain Res. Suppl.* **11**, 117–151 (1986)].
2. Rodman, H.R. & Albright, T.D. *Exp. Brain Res.* **75**, 53–64 (1989).
3. Pack, C.C., Berezovskii, V.K. & Born, R.T. *Nature* **414**, 905–908 (2001).
4. Stoner, G.R. & Albright, T.D. *Nature* **358**, 412–414 (1992).
5. Stoner, G.R. & Albright, T.D. *Vision Res.* **36**, 1291–1310 (1996).
6. Sclar, G., Maunsell, J.H.R. & Lennie, P. *Vision Res.* **30**, 1–10 (1990).
7. Ikeda, H. & Wright, M.J. *Exp. Brain Res.* **20**, 471–484 (1974).
8. Solomon, S.G., White, A.J. & Martin, P.R. *J. Physiol. (Lond.)* **517**, 907–917 (1999).
9. Krnjević, K. *Gen. Pharmacol.* **23**, 965–975 (1992).
10. Sillito, A.M. *J. Physiol. (Lond.)* **250**, 305–329 (1975).
11. Wilson, H.R. in *Visual Detection of Motion* 219–251 (Academic, San Diego, 1994).
12. Albright, T.D. *Science* **255**, 1141–1143 (1992).
13. Duncan, R.O., Albright, T.D. & Stoner, G.R. *J. Neurosci.* **20**, 5885–5897 (2000).
14. Maunsell, J.H.R., Nealey, T.A. & DePriest, D.D. *J. Neurosci.* **10**, 3323–3334 (1990).

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