

**Apostolos P. Georgopoulos, Thomas Naselaris, Hugo Merchant and Bagrat Amirikian**

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## Reply to Kurtzer and Herter

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REPLY: Our paper (Naselaris et al. 2006) examined statistically—in great detail—the distribution of a large number (>1,000) of preferred directions calculated from firing rates during free, unconstrained reaching movements in three-dimensional (3D) space. The enriched representation of forward (and to a lesser degree backward) reaching confers an obvious behavioral advantage and, very probably, is conferred on by the high frequency of occurrence of such movements in everyday life. A wealth of information from other studies, cited and discussed in our paper, supports this interpretation. All of this evidence notwithstanding, Kurtzer and Herter contend that a previous paper by Scott et al. (2001) offers the correct interpretation. However, the movements analyzed by Scott et al. (2001) were constrained to the horizontal plane, achieved by a special mechanical exoskeleton worn by the monkey. Obviously, such movements are hardly ever performed in real life (monkeys do not wear mechanical exoskeletons) and they hardly have relevance to our results. The natural state of affairs is movements in 3D space, to which motor cortical cells relate. Movements in two-dimensional (2D) space capture only a slice of this natural repertoire, as discussed previously (Amirikian and Georgopoulos 2003). Specifically, preferred directions calculated from 2D movements can come from a practically infinite number of preferred directions in 3D space (see Fig. 3 in Amirikian and Georgopoulos 2003) and are thus indeterminate with respect to which 3D preferred direction they truly reflect. Although restriction of joint motion might be useful for other objectives, they are inappropriate for analyzing the properties of the distribution of true, 3D preferred directions. Finally, why should a limit of one's ability to make a measurement be seen as an advantage? If one wishes to investigate this effect, one can profit from a recent paper on how to calculate torques in 3D for a monkey arm (Chan and Moran 2006).

Kurtzer and Herter complain that we did not discuss the paper by Scott et al. (2001) as an explanatory principle. Indeed, we are thankful to Kurtzer and Herter for reviving that paper and bringing it in focus because there are many problems with that work (see Ashe et al. 2001 for a short critique). The major point of that paper was that, under certain conditions of joint motion constraints involving only flexion and extension of the shoulder and elbow, movements can be made to targets on a plane in contrast to the prediction of the population vector. As pointed out shortly after the publication of that paper, “these findings may simply be the result of a small sampling size, the incorrect calculation of preferred directions with asymmetri-

cally distributed targets in space, or an incorrect population vector weighting function” (Ashe et al. 2001). In addition, a confined movement is much more likely to have muscle activity correlated with the direction of movement. This is explained by the fact that there are only two directions of movement at each joint and therefore off-axis forces generated by the muscles will be compensated by the external mechanical constraints of the apparatus. Because this paradigm limits the directional domain of free movements, it will bias the regressions used to calculate preferred directions and thereby skew the preferred directions. Projections of neural activity and of muscle activity onto the plane used in these experiments will amplify small nonuniformities. Any apparent nonuniformities may result from this projection.

As for a general interpretation of directional tuning, it has always been regarded as reflecting sensorimotor processes (Georgopoulos 1995; Georgopoulos et al. 1982), depending on the epoch one is examining. For example, the earliest changes in activity cannot reflect peripheral factors because none of them is operative some tens of milliseconds after stimulus onset. Nonetheless, that very early activity is directionally tuned (Georgopoulos et al. 1982) and yields the correct population vector direction (Georgopoulos et al. 1984, 1988). As the movement begins and runs its course, peripheral factors might well play a role (Fu et al. 1993). The issue is not black or white but gradations of gray (depending on the time interval) and was previously discussed in some detail (Georgopoulos 1995). In addition, recent uses of population vector decoding for neuroprosthetic control show that such information can be extracted and applied in the absence of any arm movement (Schwartz 2004; Taylor et al. 2002). In fact, directional tuning information obtained by just showing the monkey the target in the absence of movement has proved very useful for subsequent neuroprosthetic control in monkeys (Wahnoun et al. 2006) and human subjects (Hochberg et al. 2006).

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