

## LETTER TO THE EDITOR

### YES, THERE IS A HALF-CYCLE DISPLACEMENT LIMIT FOR DIRECTIONAL MOTION DETECTION

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Apparent motion of a band-pass filtered random-dot kinematogram (RDK) is seen in a sequence of two or more frames, where each trailing frame is a translated version of the preceding one. The largest displacement that produces a reliable and correct impression of directional motion is known as  $D_{\max}$ .

Current models of biological motion sensors postulate that the range of values that  $D_{\max}$  can assume is limited by half the period of the sensor's preferred spatial frequency (Adelson & Bergen, 1985; Marr & Ullman, 1981; van Santen & Sperling, 1985; Watson & Ahumada, 1985). In an apparent contradiction of this postulate, values of  $D_{\max}$  considerably greater than the half-period of the image's lowest spatial frequency have been found with isotropically-filtered RDKs (Bischof & Di Lollo, 1990; Cleary & Braddick, 1990). An account of the excessive values of  $D_{\max}$ , consistent with the half-cycle limit, can be given in terms of image frequency components at orientations oblique to the direction of motion. The frequency of such components with respect to the direction of motion is reduced by a factor of  $\cos \theta$ , where  $\theta$  is the orientation with respect to the direction of motion. Oblique components can thus raise the value of  $D_{\max}$  beyond the half-period of the filter's lower cut-off frequency.

Cleary and Braddick considered and rejected this option on the basis of results obtained with two sets of RDKs passed by different filters (Cleary & Braddick, 1987, 1990; Cleary, 1987). The two filters had the same centre-frequency (2.66 c/deg) and frequency bandwidth (1.5 octaves), but differed in orientation bandwidth ( $\alpha$ ). One filter ( $\alpha = 0$  deg) passed only components with orientation orthogonal to the direction of motion; the other ( $\alpha = 180$  deg)

passed components at all—notably oblique—orientations.

The two sets of stimuli yielded approximately equal mean values of  $D_{\max}$  (0.87 cycles of the centre frequency for  $\alpha = 0$  deg, and 0.96 for  $\alpha = 180$  deg). Equality of outcomes was regarded as inconsistent with expectations based on off-axis components. That is, any contribution to motion detection made by off-axis components should have been evidenced in greater values of  $D_{\max}$  for RDKs passed by the 180 deg filter. In the absence of such an effect, Cleary and Braddick (1987, 1990) rejected the off-axis account as an explanatory basis for the excessive values of  $D_{\max}$ . In turn, this disconfirms the assumption of the half-cycle limit and impugnes the scope and generality of current models of biological motion sensors.

These are weighty conclusions, based on evidence of relatively limited scope. To broaden the scope, we need to know to what extent predictions based on the half-cycle limit can account for performance with stimuli varying systematically in frequency and orientation bandwidths. A one-dimensional analysis, limited to single independent motion sensors, is clearly insufficient. What is needed is a two-dimensional scheme capable of describing how the outputs of populations of sensors combine to produce the observed outcome. In short, we need a model of motion integration. We report such a model and its empirical verification in the target article of the present comments (Bischof & Di Lollo, 1991).

In their comment, Braddick and Cleary (1991) question the sufficiency of our model and data in establishing the half-cycle displacement limit as a general rule of motion perception.

The objection is based largely on the tenet—discussed above—that the value of  $D_{\max}$  is not noticeably affected by image components oblique to the direction of motion. We do not concur for several reasons. First, similarity of  $D_{\max}$  for images with different oblique components does not necessarily constitute evidence against the assumption of a half-cycle displacement limit. For example, our model—predicated on such a limit—yields very similar values of  $D_{\max}$  for images passed by filters with orientation bandwidths of 0 and 90 deg (Bischof & Di Lollo, 1991, Fig. 5). The same holds for images passed by filters of any orientation bandwidth at large frequency bandwidths. The model's predictions are confirmed by the data (Bischof & Di Lollo, 1991, Fig. 4). Thus, whether  $D_{\max}$  is noticeably affected by oblique image components depends on the particular combination of other attributes of the image.

Second, pronounced effects of oblique components on  $D_{\max}$  are predicted by our model for other filter attributes that apply also to the two sets of images that Cleary and Braddick regarded as yielding approximately equal values of  $D_{\max}$ . Cleary and Braddick to the contrary, we believe that the expected differences are indeed contained in their results. The  $D_{\max}$  values of 0.87 and 0.96 cited by Braddick and Cleary (1991 see above) represent the means of three observers. The corresponding individual values (approximated from the relevant figures in Cleary, 1987, and in Cleary & Braddick, 1990) are: 0.91, 0.80 and 0.86 for  $\alpha = 0$  deg, and 1.08, 0.95 and 0.95 for  $\alpha = 180$  deg. In every case,  $D_{\max}$  is greater for images containing oblique components. This can hardly be regarded as evidence that the two sets of values are the same. The direction of the differences is as predicted by our model and as obtained by our observers (Bischof & Di Lollo, 1991, Figs 4 and 5). Combining the results of all studies, five out of five observers show differences in the expected direction.

Admittedly, the differences obtained by Cleary and Braddick are smaller than ours. Presumably, this could be due to the relatively greater effect of aliasing noise in two-frame one-dimensional ( $\alpha = 0$  deg) displays, as suggested by Braddick and Cleary (1991). But, as shown above, noise alone cannot account for the differences. To buttress this point, consider the largest differences in  $D_{\max}$  revealed in our study (Bischof & Di Lollo, 1991, Fig. 11). None of these differences can be attributed to

differential distribution of noise across channels because the corresponding images had the same frequency and orientation bandwidths. Yet, these results are naturally explained within our model in terms of contributions by oblique components. Incidentally, neither this nor other effects of orientation bandwidth can be predicted on the basis of the motion sensor proposed by Cleary and Braddick (1990); we verified this in a simulation described elsewhere (Bischof & Di Lollo, 1990).

Our reason for doing the work reported in the target article (Bischof & Di Lollo, 1991) was not to make a case for the half-cycle displacement limit. As can be readily checked by reference to the literature on motion perception, the case hardly needs to be made. Rather, our aim was to assess what additional mechanism might be required to account for the full range of motion phenomena without violating the half-cycle rule. Having examined and discarded several alternative schemes, we adopted the simple linear model of motion integration described in the target article. All the phenomena that we set out to examine are explained within this model. What is more, the model itself fits readily within a broader conceptual framework—common to current models in this area—that treats spatio-temporal filtering as the basis for motion perception. In this context, there is no call to establish the half-cycle displacement limit as a general rule of motion perception (a task that Braddick and Cleary believe we failed to achieve). Rather, if the rule is to be brought into question, valid reason and compelling evidence must be provided. We do not believe that either has been provided so far.

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