Separation in the visual field has divergent effects on discriminating the speed and the direction of motion

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eTOC blurb: Judgments of speed and direction are often thought to depend on a single velocity signal, derived from the distribution of activity in neurons specific to both attributes of motion. But Takahashi *et al* show the two types of discrimination are very differently affected by increases in the spatial separation of the moving arrays that are compared

Local motion in a visual scene allows the detection of prey or predator and predicts their future positions. Relative motion segregates objects and reveals their 3D relationships. 'Optic flow' – the motion of texture across the field – guides locomotion and balance. Given these several uses of visually perceived motion, it is unsurprising that many species have evolved hard-wired neural mechanisms to extract motion as a primitive feature of the visual world [1]. In the cortex [e.g. 2, 3, 4], and even the retina [5], of primates, cells are found that respond selectively according to direction of motion. In visual areas V1 and MT, some directionally selective cells are also tuned for the second attribute of motion, speed [3]. It might be thought that the brain derives a single velocity signal from the activity in this population of neurons – since speed and direction must often be combined to predict an object's future position or to derive a 3D structure. However, we report here a striking difference in discrimination of the two attributes: Thresholds for direction, but not those for speed, increase with the spatial separation of the stimuli.

Several previous findings hint that direction and speed may be differently computed:
(i) Direction discrimination is poorer for oblique than for cardinal directions, but this is not the case for speed [6].
(ii) Speed discrimination for arrays of random dots is of similar precision whether the two arrays move in the same, in opposite or in orthogonal directions [7].
(iii) Transcranial magnetic stimulation, applied medially, is reported to impair speed discrimination disproportionately relative to direction discrimination, under conditions where the physical stimuli and their discriminability were similar [8]

In the present experiment we asked how the precision of discriminating speed or direction changed as the spatial separation of the discriminanda increased. The stimuli were pseudo-random arrays of moving dots, briefly presented (Fig 1A). They fell on an imaginary circle (radius: 5 degrees of visual angle) centred on the fixation point [7]. The spatial separation of the two arrays varied between blocks and had a maximal value of 10 degrees of visual angle – while their eccentricity remained constant.
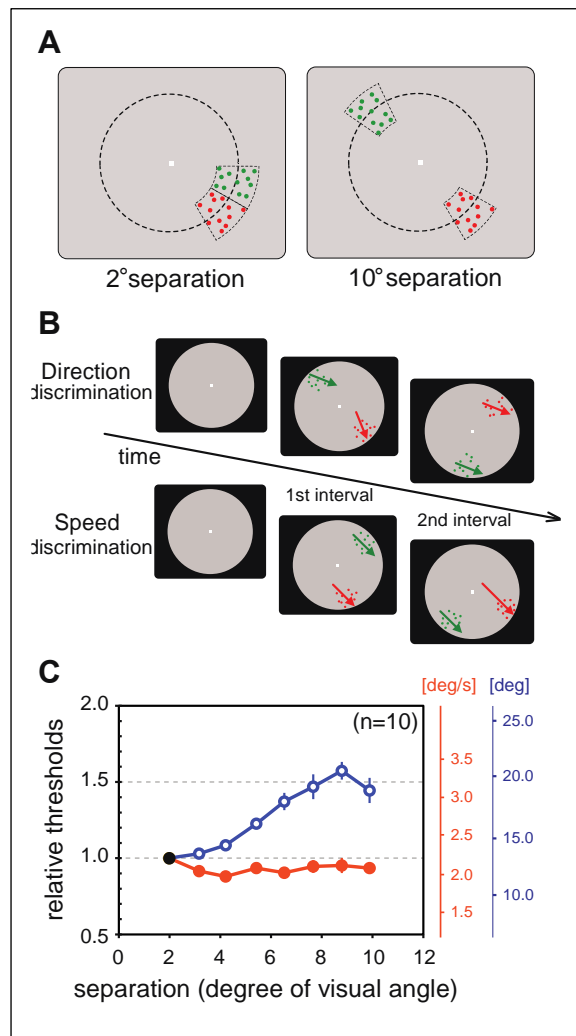

Figure 1. **Stimuli and results for discriminating direction and discriminating speed.**

(A) Spatial arrangement of the stimuli. The two arrays of random moving dots fell on an imaginary circle centred on the fixation point. In different blocks of trials, the separation of the midpoints of the two arrays varied from 2° (when their edges touched) to 10° (when they fell on a diameter of the imaginary circle). The dashed and dotted lines in this diagram were not present in the actual display. (B) Temporal arrangement. In one of two 180-ms intervals, separated by 500 ms, the arrays of dots were identical in speed and direction, and in the other, selected at random, they differed either in direction or (in interleaved experimental runs) in speed. Participants were asked to report the interval in which a difference was present. A steady white background field of 10 cd.m-2 was present throughout. (C) Results for the two interleaved series of measurements. Thresholds for detecting a difference in direction of motion (open circles) or in speed (filled circles) are shown as a function of the spatial separation of the mid-points of the arrays (see Panel A). Thresholds for the two types of discrimination are normalised to 1.0 at the minimal separation. The secondary ordinates to the right show numerical values for the two tasks. Error bars represent ±1 SEM

In alternating runs, we measured the discrimination of the two attributes. In both cases, the participant's task was chosen to be the simplest possible: detection of the presence of a difference. In one of two intervals (Fig 1B), the two arrays moved in the same direction and at the same speed; in the other, they differed in speed or in direction according to the condition tested. An adaptive procedure estimated the stimulus difference that supported 79.4% correct (See Supplementary Methods). The reference speed at which discrimination was measured was 5 deg.s-1 and the reference direction was 135° from vertical (4.30 o'clock).

Normalised average thresholds for 10 participants are shown in Fig 1C as a function of the spatial separation of the two arrays of moving dots. A striking difference is seen between the results for discrimination of direction and for discrimination of speed. Thresholds for detecting a difference in *direction* (open circles) increase systematically

with the spatial separation of the two arrays (One-way Repeated Measures ANOVA (after Greenhouse-Geisser correction): $F_{(2.739, 24.652)}=18.44$, $p<.001$). In contrast, thresholds for *speed* (closed circles) vary little with separation – a result we previously found for discrimination of spatial frequency. In fact, a one-way Repeated Measures ANOVA with Greenhouse-Geisser correction does show a marginally significant effect of separation ($F_{(3.181, 28.628)}=3.414$, $p=.029$), owing probably to the *higher* thresholds for abutting arrays. The latter effect may reflect compulsory pooling of local signals [7].

How should we explain this difference between the two types of discrimination concurrently measured with closely similar stimuli? In the case of direction, we may suppose that the observer's judgement is based on a difference signal extracted early in the visual system by 'comparator neurons' that are hard-wired to detect contrast of motion direction. An analogy can be made here with the most familiar type of comparator neuron known to visual science – a centre-surround retinal ganglion cell that draws excitatory input from receptors in the centre of its receptive field and inhibitory input from the surround. Such a cell signals local contrast of luminance to the brain; and it is likely to be signals originating in such cells that observers use in equating the two halves of a photometric field. It is notable that discrimination of luminance deteriorates as the two half-fields are separated [see e.g. 9].

Neurons are found in primate visual cortex that respond strongly to local contrast in motion direction [e.g. 4] and it may be on such signals that observers similarly depend for object segregation and the derivation of 3D structure. It is plausible that such local contrast signals would become weaker the greater the spatial separation of the stimuli; and so we may suspect that our participants, in detecting a difference in motion direction, rely on contrast signals originating in dedicated comparator neurons. Since we deliberately asked observers only to identify the interval containing a difference, it is not necessary that the hypothesised neural signal preserves the sign of the difference: it may represent only the presence of a discontinuity.

But what is happening in the case of speed? Reports of cortical neurons sensitive to local contrast of speed – to shearing stimuli – are rarer but can certainly be found [e.g. 2 Fig. 2]. However, we might plausibly expect such neurons to respond more weakly when the stimuli lie far apart. Since a difference in speed can be detected with similar precision over a large range of separations, we propose that discrimination in this task does not depend on difference signals originating in hard-wired comparator neurons early in the visual system that signal local contrast of speed. Instead, our working hypothesis is that discrimination of speed here depends on two independent signals that are delivered to the site of comparison encoded in abstract, symbolic representations. As in the 'object files' postulated by Treisman [10], these symbolic representations would include the spatial coordinates of the individual stimuli. (See ref 7 for a development of this account of discriminations that are independent of the spatial separation of the stimuli.)

But theory apart, Figure 1 reveals a firm empirical difference in the discrimination of direction and speed.

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