

Factors affecting footsteps: contrast can change the apparent speed, amplitude and direction of motion

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Abstract

Contrast can affect the apparent speed of a moving stimulus [P. Thompson, Ph.D. thesis, University of Cambridge, Cambridge, UK, 1976; *Vis. Res.* 22 (1982) 377; *Perception* 28 (1999) 33]. Specifically, when a grey square drifts steadily across stationary black and white stripes, it appears to stop and start as its contrast changes—the so-called ‘footsteps illusion’ [*Perception* 30 (2001) 785; *Neural Networks* 16 (2003a) 933; S.M. Anstis, Levels of motion perception, in: L. Harris, M. Jenkin (Eds.), *Levels of Perception*, Springer, New York, 2003b, p. 75]. We now show that what matters is the contrast of the leading and trailing edges, not of the lateral edges. The stripes act by altering the stimulus contrast, and are not merely stationary landmarks. Back and forth apparent motion appears smaller in amplitude at low contrasts, even on a spatially uniform (non-striped) surround, and this is a specific motion phenomenon, not a result of misjudging static position. Contrast also affects the perceived direction of a moving stimulus. A vertically jumping grey diamond on a surround of black and white quadrants appears to change its direction of movement depending on the relative contrast of its left-oblique versus right-oblique edges against the surround. Thus, the perceived direction, amplitude and speed of moving objects depend greatly on their luminance contrast against the surround. A model of motion coding is proposed to explain these results.

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1. Introduction

There is a wealth of evidence that the apparent velocity of a moving object varies with its contrast (Anstis, Smith, & Mather, 2000; Blakemore & Snowden, 1999, 2000; Campbell & Maffei, 1981; Gegenfurtner & Hawken, 1996; Hawken, Gegenfurtner, & Tang, 1994; Stone & Thompson, 1992; Thompson, 1976, 1982; Thompson & Stone, 1997; Thompson, Stone, & Brooks, 1995). In particular, Anstis (2001, 2003a, 2003b) found that an object moving at constant speed across a variegated background can appear to change its apparent speed in ‘real time’ as its contrast changes. He called this phenomenon the ‘footsteps illusion’. A grey square that drifts horizontally across a surround of black and white vertical stripes appears to stop and start as it crosses each stripe. A dark grey square appears to slow down on

a black stripe, where its edges have low contrast, and to accelerate on a white stripe, where its edges have high contrast. Conversely a light grey square appears to slow down on a white stripe and to accelerate on a black stripe (Fig. 1). Thus, the apparent speed of a moving edge depends on its instantaneous *contrast* against the background.

We call this the ‘footsteps illusion’, because the light and dark gray squares appear to speed up and slow down in alternation, like the two feet of a walker. The effect is striking and robust, particularly in peripheral vision, when the squares can appear to come briefly to a complete standstill on each cycle. This raises a host of questions, including:

1. *Nature of the illusion.* Exactly what is changing perceptually? Is it the perceived speed? Or the perceived spatial, or temporal extent of the motion? (speed = distance/time). Or do the two squares merely vary in their relative latency, rather than relative velocity?

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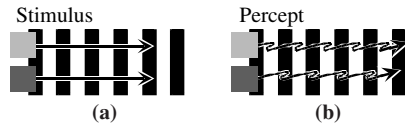


Fig. 1. (a) A light and a dark grey square move smoothly in step across stationary black and white stripes. (b) The dark grey square appears to slow down on a black stripe, where its edges have low contrast, and to accelerate on a white stripe, where its edges have high contrast. The opposite is true for the light grey square (after Anstis, 2001).

2. *Sufficient and necessary conditions.* Do the edges of the stripes act as local landmarks that apparently speed up the squares as they pass over these edges, regardless of contrast? Does the background need a spatial structure at all? Must the motion be ‘real’ (continuous), or can the illusion alter the appearance of ‘apparent’ motion that jumps back and forth across a fixed distance?
3. *Coding mechanisms.* What forms of motion coding might explain the footsteps illusion?

This paper will address some of these questions.

Our three experiments will show that varying the luminance contrast of a moving square alters its perceived speed, not merely its perceptual latency. Experiment 1 shows that the leading and trailing edges of the moving squares are much more important than the side edges, whilst Experiments 2 and 3 show that contrast affects the subjective appearance of back and forth apparent motion—its amplitude in Experiment 2 and its direction in Experiment 3. At the end I shall present a simple model of motion coding.

2. Experiment 1: Spatial factors in the squares. Leading and trailing edges are more important than lateral edges

Which *parts* of the moving squares interact with the stationary background to produce the illusion? I teased apart the role of the leading and trailing edges of the moving squares versus their lateral (top and bottom) edges by showing three different stimuli to a class of 150 undergraduate students who were sitting in a large classroom and viewed the stimuli on a screen from a wide range of viewing distances and viewing angles. They were asked to rate the perceived movement on a scale from zero to ten. In the control condition (Fig. 2a) the two squares, one light and one dark, drifted horizontally across a large striped surround. This gave a strong footsteps illusion, which the students were instructed to rate as a ten. They were told that completely smooth motion should get a rating of zero. In a ‘railroad track’ condition, the squares ran along a striped ‘track’ of the same vertical height as the stripes (Fig. 2b), so that the leading and trailing edges moved over the sur-

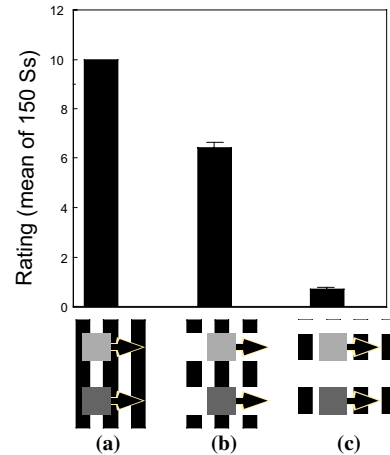


Fig. 2. 150 Students rated the strength of the variations in apparent speed when the moving gray squares contacted the stationary background stripes. (a) along all their edges, (b) along leading and trailing edges only, (c) along lateral edges only. See text.

round stripes but the lateral edges at top and bottom of the figure did not. This stimulus received a high mean rating of 6.38 ± 0.13 SE. Admittedly it is not clear why this rating came out lower than the 10 for Fig. 2a.

In a condition that resembled a ‘clearing in a forest’, the squares ran along a clear white ‘track’ cut through the surround grating so that the stationary stripes abutted only the lateral edges, not the leading and trailing edges, of the squares (Fig. 2c). Now the illusion almost disappeared and the ratings fell almost to zero (actually to $0.68 + 0.075$ SE). We conclude that it is the motion contrast of the leading and trailing edges, not the lateral edges, of the moving squares that produces the footsteps illusion.

3. Experiment 2: Contrast affects apparent amplitude of back and forth apparent motion

In our previous paper (2001) a light and a dark square moved continuously to the right across a surround of black and white vertical stripes. Now, in Experiment 2, a light or dark gray square jumped back and forth in apparent motion between two positions across a spatially uniform mid-grey surround. We examined the effects of contrast on this back- and-forth apparent motion in peripheral vision, with all stripes and landmarks removed (Fig. 3). To anticipate, this yielded two pieces of information:

1. The footsteps illusion can apply to apparent as well as to real movement.
2. The illusion can perceptually change the *amplitude* of the constant-size back and forth jumps.

A square of pre-settable gray jumped back and forth in apparent motion on a surround of a fixed mid-gray.

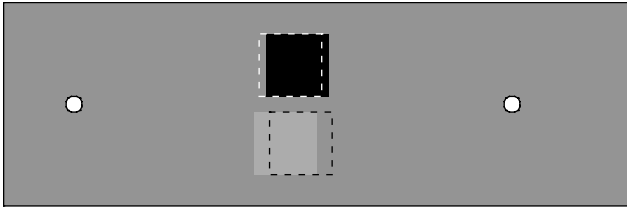


Fig. 3. Stimulus for Experiment 2. Lower grey square, of side 2.5° , jumped back and forth through 0.7° . Its luminance (and contrast) varied across trials. Observer adjusted amplitude of motion of upper black square to a subjective match. Mean retinal eccentricity was always 5.5° .

The observer's task was to judge the apparent amplitude of this motion as a function of the square's luminance, by means of a matching method. Just above the square a second, comparison black square jumped back and forth on a parallel path, but in the opposite direction (in counterphase), to reduce any perceptual locking together. The observer could adjust the amplitude of the black square's jump one pixel at a time, by hitting an 'increase' and a 'decrease' key, until satisfied that the two squares had the same apparent amplitude of motion. S/he then struck the space bar, and the setting was recorded.

The maximum obtainable luminance on the screen was 95.4 cd m^{-2} . This was designated as "white" or 100%, and all screen luminances were converted to percentages of this maximum.

The gray surround was fixed at a luminance of 31.8 cd m^{-2} (33.4% of the maximum white). The luminance of the standard square was randomly set on successive trials to one of 26 values, ranging from 0.3% to 100%. Note that as the luminance of the square increased from black through mid-gray to white, its Michelson contrast started high when it was black, then fell to zero when the square had the same luminance as the surround, then rose again as the square increased toward white.

The display was viewed from a distance of 57 cm in a dimly lit room. Luminances were calibrated with a Minolta II chromameter and a Photo Research PR 650 photometer. Distances were measured directly on the screen with a ruler.

Each square was 2.5° wide and jumped back and forth at an alternation rate of 2.5 Hz. The grey standard square jumped through a fixed distance of 0.7° whilst the black comparison square jumped through a variable distance under the control of the observer. Two fixation points were placed symmetrically to left and right, along a horizontal line between the two squares. These fixation points were 11° apart horizontally, so that the jumping squares had a mean retinal eccentricity of 5.5° . The observer switched fixation points between trials, to reduce unwanted adaptation effects.

Results for two observers are shown in Fig. 4. In Fig. 4, the luminance of the jumping squares is again expressed as a percentage of the maximum screen luminance of 95.4 cd m^{-2} , and the apparent jump sizes are expressed as a percentage of the actual jump size of 0.7° . Data shown are mean of 8 trials ± 1 SE, and lines were fitted by eye. Filled (open) symbols show squares that were darker (lighter) than the surround.

Fig. 4 shows that although the gray squares always jumped through the same distance (0.7°) their perceived amplitude depended strongly upon their log luminance, reaching a maximum for a black or white square and falling to 30% for observer FH, and close to 0% for SA, when the square approached the same luminance as the surround, that is, as the contrast approached zero.

The luminance of each square was then converted into its Michelson contrast, using the formula

$$\text{Michelson contrast} = \text{abs}(G + S_d)/(G - S_d)$$

where G is the luminance of the gray squares and S_d is the luminance of the fixed surround. These converted data from Fig. 4 are replotted in Fig. 5. Fig. 5 shows

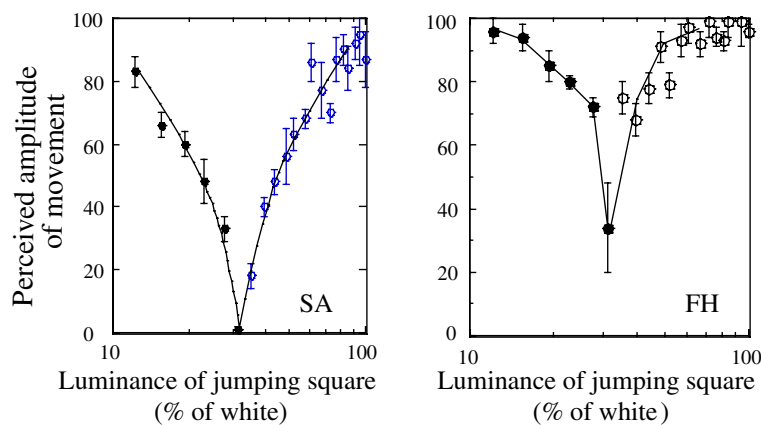


Fig. 4. Results of Experiment 2. x -axis = luminance of jumping square. When $x \approx 31.8\%$ the square's luminance matches the surround, its contrast approaches zero, and so does the perceived amplitude of its apparent motion.

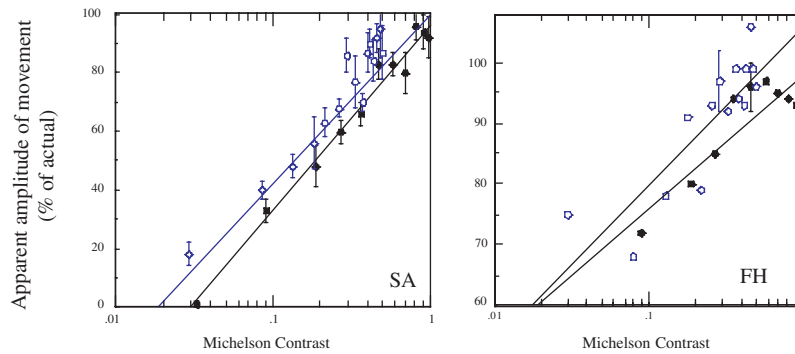


Fig. 5. Data replotted from Fig. 4 show that perceived amplitude is a linear function of log stimulus contrast. Note different ordinate scale for the two observers.

that the perceived amplitude was a linear function of log Michelson contrast. These results show that in peripheral vision, the physically constant path length of a jumping square can appear to change from 100% down to near zero as stimulus contrast is reduced.

Motion or position? The results of Experiment 2 suggest an apparent compression of the motion path length at low contrasts. But there is an alternative possible interpretation. Suppose that the *static* positions of the two end points were mis-perceived; if these somehow looked displaced toward each other at low contrasts, the illusion would be of position and not specifically of motion. Thus the observer might be converting the ostensible motion judgment into a position judgment, by covertly lining up the perceived end-positions of the black and gray squares. So we ran control experiments to rule out this possibility, by asking observers to judge the position of a single *stationary* gray square, by aligning it with an adjustable black square.

Previously the gray square jumped back and forth between two fixed positions, but now it was stationary, was randomly assigned to one of these two positions, and stayed there throughout the trial. The observer moved a single, upper black comparison square by striking a 'leftward' and a 'rightward' key until satisfied that the two squares appeared to line up vertically, and the position of the black square was recorded for later analysis. For the next trial the gray square was changed to a new randomly selected luminance (chosen from 26 possibilities) and a new random position (chosen from 2 possibilities), and further data were collected. The fixation point was randomly placed 5.5° to the left or right of the stimulus.

To cut a long story short, we found that varying the contrast *never* shifted the mean perceived positions (2 observers \times 26 trials). This implies that the motion underestimates that we previously found at low contrasts were truly judgments of motion per se, not of position. It also suggests that the motion is coded in a separate neural channel from position, rather than motion being computed by a neural 'clock and ruler' based

upon the equation $\text{velocity} = \text{distance}/\text{time}$. This harks back to Exner's (1875) original claim that motion is a sensation separate from position. He concluded this from his observation that two successive sparks can give apparent motion even when they are too close to be resolved when presented simultaneously. Similarly, when two nearby points are flashed simultaneously in the peripheral retina they cannot be resolved, but when flashed in sequence they give a strong sensation of movement—the so-called fine-grain motion illusion—(Foster, 1977; Foster & Gravano, 1989; Foster, Thorson, McIlwain, & Biederman-Thorson, 1981). We use a different method to reach a similar conclusion—namely, that position and motion are handled by different neural pathways.

4. Experiment 3: Direction of 2-D apparent motion

In Experiment 1 we showed that the leading and trailing edges of a moving square, which were influenced by contrast, can act *independently* from the lateral edges, which were not. In Experiment 3, on the other hand, a diamond moved vertically, in a direction at 45° to the orientation of its sides. We shall show that the sides can *cooperate* in determining the mean apparent direction in which the whole diamond moves. Normally, when we see a diamond move vertically downwards, the movement of the left-oblique and right-oblique sides are ambiguous because of the so-called 'aperture problem', yet we are able to combine the ambiguously moving edges into an unambiguously moving polygon. This is probably achieved by an 'intersection of constraints' method (Adelson & Movshon, 1982). We shall show here that these edge constraints are weighted in value by stimulus contrast before being combined into a perceived motion of the whole polygon.

A light grey diamond of side 6° jumped up and down through a vertical distance of 36 arcmin (one-tenth of its own diameter). On a uniform surround the motion path would be correctly seen as vertical. However, we posi-

tioned the diamond on a surround of (say) black and white quadrants in such a way that its top-left and bottom-right edges lay on black quadrants. Since the diamond was light grey, these edges had high contrast so their motion component was subjectively magnified. The other two edges lay on white quadrants. These edges had low contrast so their motion component was subjectively diminished. As a result, the motion path appeared to be tilted counterclockwise away from the vertical, in a direction that favoured the high-contrast motion component. The observer’s task was to null out this perceived direction of motion until it appeared subjectively vertical, by striking either a “rightward” or a “leftward” key on the keyboard that rotated the axis of motion clockwise or counterclockwise from the vertical, one pixel at a time. When the observer was satisfied that the motion appeared to be vertical, s/he pressed the space bar, which recorded the diamond’s luminance and the motion offset. All stimuli were displayed on a 17-in. monitor controlled by a Macintosh G4 computer and viewed from a distance of 57 cm in a dimly lit room.

On each trial the luminance of the diamond was set to a new randomly chosen value between 1% and 100% of the screen’s maximum luminance. Four surround conditions were used. The quadrants in the surround were either black and white (1% and 100%), as already stated, or else different shades of grey: 14% and 33%, or 33% and 54%, or 54% and 77%.

The luminance values of the diamonds against the quadrants were converted into Michelson contrast ratios, as follows:

Michelson contrast of the diamond luminance G against the luminance L of the lighter quadrants of the surround

$$= (L - G)/(L + G)$$

Michelson contrast of the diamond luminance G against the luminance D of the darker quadrants of the surround

$$= (D - G)/(D + G)$$

Therefore the contrast ratio

$$= [(L - G)/(L + G)]/[(D - G)/(D + G)]$$

When the contrast ratio = 1, all four edges had the same Michelson contrast against the surround and the diamond was correctly seen as moving vertically. The further the contrast ratio was away from unity, the more the perceived direction of motion appeared to deviate from the vertical. We calculated the motion ratio, which is simply the ratio of the -45° to the $+45^\circ$ component of the perceived motion (Fig. 6b). This ratio would be unity if there were no illusion, and would be less or greater than +1 for illusory deviations clockwise or counterclockwise.

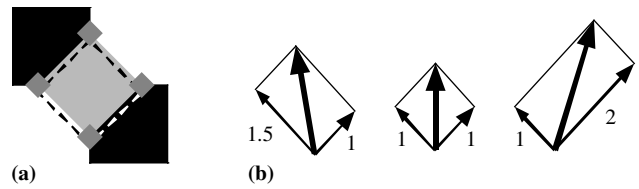


Fig. 6. (a) Stimulus for Experiment 3. A diamond jumps back and forth vertically: its lower position is shown as a dashed outline. Stationary light and dark quadrants in the surround bestow different contrasts on orthogonal edges, which distorts its perceived direction of motion. Small occluders hide the corners of the diamond. (b) Examples of perceived motion directions: motion ratios of 1.5:1, 1:1 and 1:2 (see Fig. 7).

4.1. Results

Fig. 7 shows, on a log–log plot, the relationship between the ratio of the Michelson contrast of the orthogonal sides of the diamond, versus the resulting illusory motion ratio. The combined results are shown for all four surround conditions and for the two observers SA and JB. The x -axis shows the log of the Michelson contrast ratio of the orthogonal edges of the diamond. The y -axis shows the log of the motion ratio of these edges. The data for all four surround conditions, all diamond luminances, and both observers, are plotted on a single graph. Despite a certain amount of scatter ($R^2 = 0.544$), which we attribute to the fact that data were collected on different days in many different luminance conditions, the whole data set for both observers can be fitted reasonably well by a single straight line with a slope of 0.60. This straight line on a

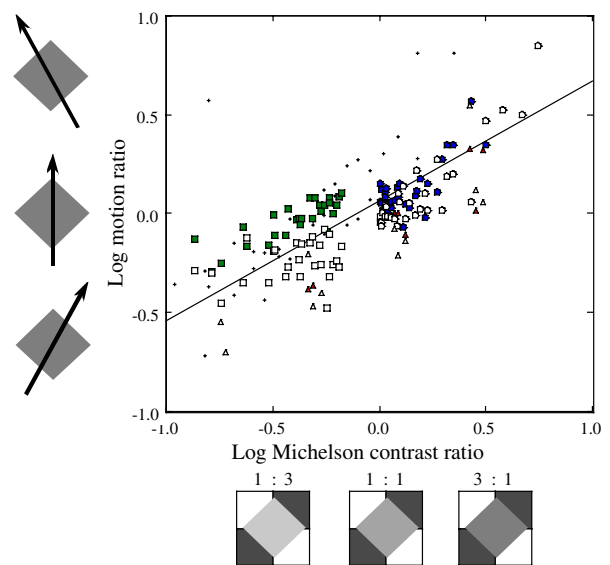


Fig. 7. Results of Experiment 3. x = Michelson contrast ratio of the two sides of the jumping diamonds. y = direction of the diamond’s perceived motion.

log–log plot represents a power law with an exponent of 0.6, so

Perceived edge motion

$$\simeq k * \text{actual edge motion} * \text{contrast}^{0.6}$$

where k is a constant of proportionality. This implies that if one edge of the diamond had twice the contrast of the other, the observer would null it out by making the lower-contrast edge move through 1.52 times the distance of the higher-contrast edge ($2^{0.6} = 1.52$).

4.2. Discussion

Despite some individual differences, both observers overestimated high contrast motion and underestimated low contrast motion. So, over a wide range of luminances, the direction in which the diamond appeared to move depended on the relative contrasts of its edges. We draw two conclusions:

- Contrast modifies the perceived *amplitude* of motion, not merely its *latency*. Any latency difference between different edges would have moved the diamond along an upright ellipse (a Lissajou figure), but it would not have tilted its path away from the vertical as we found.
- Contrast modifies the amplitude of the perceived motion of each edge *before* the edge motions are combined by an intersection of constraints (Adelson & Movshon, 1982).

5. General discussion

What visual codes for motion will be susceptible to distortion by stimulus contrast? (Mather (1994) has reviewed models of motion detectors). I regard the footsteps illusion as the motion analogue of the Bezold–Brücke hue–intensity effect in color vision (Bezold, 1873; Brücke, 1878). This is illustrated in Fig. 8a. Suppose that a monochromatic yellow light stimulates a G cone and an R cone equally at a fairly low photopic luminance. If the luminance is increased, then ideally the R cone and G cone will increase their firing rate by the same amount. In practice, however, non-linearities creep in, and the gain of (say) the R cone increases with luminance faster than the gain of the G cone. As a result, a high-intensity yellow stimulates the R cone disproportionately more than the G cone, and looks orange. This example is a simplified cartoon of the Bezold–Brücke hue shift, which actually takes place largely within color-opponent P cells in the retina (Ejima & Takahashi, 1984) and in the lateral geniculate nucleus (Valberg, Lange-Malecki, & Seim, 1991). Fry (1983) claims that the shifts are toward blue and yellow and away from purple and

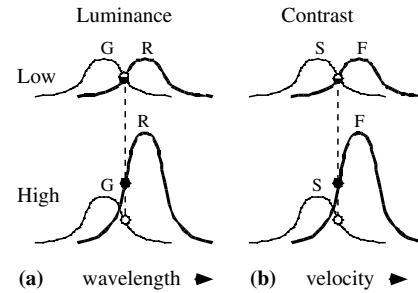


Fig. 8. (a) Cartoon of the Bezold–Brücke effect. At low luminances, a given monochromatic yellow stimulates R and G retinal cones equally (piebald spot). At high luminance, if the R cone increases its gain faster than the G cone, the same yellow would stimulate R (black spot) more strongly than G (open spot) and look orange. (b) Two *hypothetical* cells in MT are tuned to ‘slow’ and ‘fast’ velocities. At low contrast, a given medium velocity stimulates Slow and Fast channels equally. At high contrast, if the Fast channel increases its gain faster than the Slow channel, the same medium velocity would stimulate F (black spot) more strongly than S (open spot) and look faster.

green. In general, with increasing luminance reds and green shift toward yellow, and blues and blue-greens shift toward blue. Pridmore (1999) provides an extensive recent study.

I propose a similar scheme for motion coding, based upon visual neurons in MT that are tuned to a preferred range of velocities, as described by Maunsell and Van Essen (1983). The response of such cells also depends upon stimulus contrast (Ohzawa, Sclar, & Freeman, 1985). In Fig. 8b, two *hypothetical* neurons in MT are tuned, respectively, to fast and slow motion. At a low contrast, a given medium speed stimulates both channels equally. If the contrast (not luminance) is increased, then both the fast and the slow channel will increase their firing rate, ideally by the same amount. In the model, however, non-linearities creep in, and the gain of the fast channel increases with contrast more than the gain of the slow channel. Consequently, at high contrast the same medium velocity as before now stimulates the fast channel disproportionately more than the slow channel, and the motion looks subjectively faster. Note that in the Bezold–Brücke phenomenon, x = luminance, y = hue, whilst in our effects x = contrast, y = strength of motion signal.

Another possible analogue is the pitch–intensity relationship in hearing. Stevens (1935) and Gulick (1971) both found that a high-frequency tone sounds even higher when its intensity is raised. Gulick found that when a 7000 Hz tone was increased in intensity from 30 to 70 dB SL, it appeared to rise in pitch by 115 Hz.

I attribute this to auditory recruitment. Notice that hearing sensitivity is falling off rapidly as frequency increases in the region of 7000 Hz. Imagine an organism whose hearing curve is supported by a neural unit tuned to 7000 Hz and an intensity threshold of I , plus a less

sensitive unit tuned to (say) 7100 Hz and an intensity threshold of $2 * I$. A 7000 Hz tone of intensity I will just stimulate the 7000 Hz unit. As its intensity increases to $2 * I$ and beyond, it will begin to recruit the less sensitive 7100 Hz unit. Assuming that pitch is coded as the centroid of action in a family of tuned units, this will shift the perceived pitch from 7000 up toward 7100 Hz. (A similar account can be given for low tones: as a low frequency tone increases in intensity, it sounds even lower (Gulick, 1971; Stevens, 1935). I argue that it recruits less sensitive units that are tuned to even lower frequencies, causing the perceived pitch to fall.)

However, it is unlikely that the footsteps illusion is analogous to the pitch–intensity effect. If it were, then the strongest contrast–motion effect would arise from recruitment of less sensitive motion detectors at the top end of detectable speeds—namely, at high velocities. However, Pete Thompson has found (personal communication) that the contrast–motion effect fades out at high velocities.

Note that the contrast dependence of motion is a far bigger effect than the modest Bezold–Brücke or pitch–intensity phenomena. The Bezold–Brücke effect is small and seems to be a minor design fault caused by non-linearity. On the other hand, particularly in peripheral vision, a grey square can almost appear to stop dead as it moves over black and white stripes.

For a more detailed and sophisticated model along these lines (see Chey, Grossberg, & Mingolla, 1997, 1999). Their neural network model represents visual velocity as a distributed population code of speed-tuned units, in which the size of a unit's receptive field is correlated with its preferred speed and with its threshold. Their model successfully simulates many of Thompson's discoveries of increased perceived speed at higher contrasts (Grossberg, Mingolla, & Viswanathan, 2001).

In conclusion, let us summarise our results and see how far they answer the questions with which we started. Experiment 1 examined spatial factors in the squares, and showed that leading and trailing edges are more important than lateral edges. Experiments 2 and 3 examined the effects of contrast upon back and forth apparent motion. These showed that continuous real motion was not necessary. In Experiment 2, contrast altered the perceived amplitude, and in Experiment 3 altered the perceived 2-D direction, of back and forth apparent motion. Together, the experiments ruled out any serious role for perceptual latency, and they confirmed that contrast could affect perceived speed, amplitude and direction. Finally, the effects of contrast upon perceived speed are consistent with a hypothetical coding scheme of channels tuned to different velocities, such that the gain increases more rapidly in fast than in slow channels as contrast increases—a motion analogue of the Bezold–Brücke effect for color.

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References

- Adelson, E. H., & Movshon, J. A. (1982). Phenomenal coherence of moving visual patterns. *Nature*, *300*, 523–525.
- Anstis, S. M. (2001). Footsteps and inchworms: Illusions demonstrate that contrast modulates motion salience. *Perception*, *30*, 785–794.
- Anstis, S. M. (2003a). Moving objects appear to slow down at low contrasts. *Neural Networks*, *16*, 933–938.
- Anstis, S. M. (2003b). Levels of motion perception. In L. Harris & M. Jenkin (Eds.), *Levels of perception* (pp. 75–99). New York: Springer.
- Anstis, S. M., Smith, D. R., & Mather, G. (2000). Luminance processing in apparent motion, Vernier offset and stereoscopic depth. *Vision Research*, *40*, 657–675.
- Blakemore, M. R., & Snowden, R. J. (1999). The effect of contrast upon perceived speed: A general phenomenon? *Perception*, *28*, 33–48.
- Blakemore, M. R., & Snowden, R. J. (2000). Textured backgrounds alter perceived speed. *Vision Research*, *40*, 629–638.
- Brücke, E. (1878). Über einige Empfindungen im Gebiete des Sehnerven. *Sitzungsbereich der Akademie der Wissenschaft in Wien*, *77*, 39–71.
- Campbell, F. W., & Maffei, L. (1981). The influence of spatial frequency and contrast on the perception of moving patterns. *Vision Research*, *21*, 713–721.
- Chey, J., Grossberg, S., & Mingolla, E. (1997). Neural dynamics of motion grouping: From aperture ambiguity to object speed and direction. *Journal of the optical Society of America*, *14*, 2570–2594.
- Chey, J., Grossberg, S., & Mingolla, E. (1999). Neural dynamics of motion processing and speed discrimination. *Vision Research*, *38*, 2769–2786.
- Ejima, Y., & Takahashi, S. (1984). Bezold–Brücke hue shift and nonlinearity in opponent-color process. *Vision Research*, *24*, 1094–1097.
- Exner, S. (1875). Experimentelle Untersuchungen der einfachsten psychischen Prozesse. *Pflügers Archiv Physiologie*, *62*, 423–432.
- Foster, D. H. (1977). Rod- and cone-mediated interactions in the fine-grain movement illusion. *Vision Research*, *17*, 123–127.
- Foster, D. H., Gravano, S., & Tomoszek, A. (1989). Acuity for fine-grain motion and for two-dot spacing as a function of retinal eccentricity: Differences in specialization of the central and peripheral retina. *Vision Research*, *29*, 1017–1031.
- Foster, D. H., Thorson, J., McIlwain, J. T., & Biederman-Thorson, M. (1981). The fine-grain movement illusion: A perceptual probe of neuronal connectivity in the human visual system. *Vision Research*, *21*, 1123–1128.
- Fry, G. A. (1983). The Bezold–Brücke phenomena at the two ends of the spectrum. *American Journal of Optometry and Physiological Optics*, *60*, 977–981.
- Gegenfurtner, K. R., & Hawken, M. J. (1996). Perceived velocity of luminance, chromatic and non-Fourier stimuli: Influence of contrast and temporal frequency. *Vision Research*, *36*, 1281–1290.

- Grossberg, S., Mingolla, E., & Viswanathan, L. (2001). Neural dynamics of motion integration and segregation within and across apertures. *Vision Research*, 41, 2521–2553.
- Gulick, W. L. (1971). *Hearing: Physiology and psychophysics*. Oxford University Press.
- Hawken, M. J., Gegenfurtner, K. R., & Tang, C. (1994). Contrast dependence of colour and luminance motion mechanisms in human vision. *Nature (London)*, 367, 268–270.
- Mather, G. (1994). Motion detector models: Psychophysical evidence. In A. T. Smith & R. Snowden (Eds.), *Visual detection of motion* (pp. 117–144). London: Academic Press.
- Maunsell, J. H. R., & Van Essen, D. (1983). Functional properties of neurons in idle temporal visual area of the macaque monkey. I. Selectivity for stimulus duration, speed, and orientation. *Journal of Neurophysiology*, 49, 1127–1147.
- Ohzawa, I., Sclar, G., & Freeman, R. D. (1985). Contrast gain control in the cat's visual system. *Journal of Neurophysiology*, 54, 651–667.
- Pridmore, R. W. (1999). Bezold–Brücke hue shift as functions of luminance level, luminance ratio, interstimulus interval and adapting white for aperture and object colors. *Vision Research*, 39, 3873–3891.
- Stevens, S. S. (1935). The relation of pitch to intensity. *Journal of the Acoustical Society of America*, 6, 150–154.
- Stone, L. S., & Thompson, P. (1992). Human speed perception is contrast dependent. *Vision Research*, 32, 1535–1549.
- Thompson, P. (1976). *Velocity aftereffects and the perception of movement*. PhD thesis, University of Cambridge, Cambridge, UK.
- Thompson, P. (1982). Perceived rate of movement depends on contrast. *Vision Research*, 22, 377–380.
- Thompson, P., & Stone, L. S. (1997). Contrast affects flicker and speed perception differently. *Vision Research*, 37, 1255–1260.
- Thompson, P., Stone, L. S., & Brooks, K. (1995). Speed perception in the fovea is not always independent of contrast. *Perception*, 24(Suppl.), 2.
- Valberg, A., Lange-Malecki, B., & Seim, T. (1991). Colour changes as a function of luminance contrast. *Perception*, 20, 655–668.
- von Bezold, W. (1873). Über das Gesetz der Farbenmischung und die physiologischen Grundfarben. *Poggendorffs Annalen*, 150, 221–239.