

Correction

PSYCHOLOGICAL AND COGNITIVE SCIENCES

Correction for “Default perception of high-speed motion,” by Mark Wexler, Andrew Glennerster, Patrick Cavanagh, Hiroyuki Ito, and Takeharu Seno, which appeared in issue 17, April 23, 2013, of *Proc Natl Acad Sci USA* (110:7080–7085; first published April 9, 2013; 10.1073/pnas.1213997110).

The authors wish to note that the description of the stimuli in experiments 2–4 was partly erroneous. In particular, the stimuli were described as continuing to turn after the visual transient, in the final phase of each trial. In all cases, the stimuli remained still after the transient. In experiment 2, the stimuli remained visible until the participant’s response. In experiments 3 and 4, the stimuli remained stationary and visible for 400 ms after the transient, at full contrast for the first 200 ms and then fading out for the last 200 ms. This error does not affect the conclusions of the article, most of which can be readily verified by viewing the online demonstrations.

www.pnas.org/cgi/doi/10.1073/pnas.1511553112

Default perception of high-speed motion

Mark Wexler^{a,1}, Andrew Glennerster^b, Patrick Cavanagh^a, Hiroyuki Ito^c, and Takeharu Seno^{c,d}

^aLaboratoire Psychologie de la Perception, Université Paris Descartes and Centre National de la Recherche Scientifique, 75006 Paris, France; ^bSchool of Psychology and Clinical Language Sciences, University of Reading, Reading RG6 6AL, United Kingdom; and ^cFaculty of Design and ^dInstitute for Advanced Study, Kyushu University, Fukuoka 812-8581, Japan

Edited by George Sperling, University of California, Irvine, CA, and approved March 19, 2013 (received for review August 18, 2012)

When human observers are exposed to even slight motion signals followed by brief visual transients—stimuli containing no detectable coherent motion signals—they perceive large and salient illusory jumps. This visually striking effect, which we call “high phi,” challenges well-entrenched assumptions about the perception of motion, namely the minimal-motion principle and the breakdown of coherent motion perception with steps above an upper limit called d_{\max} . Our experiments with transients, such as texture randomization or contrast reversal, show that the magnitude of the jump depends on spatial frequency and transient duration—but not on the speed of the inducing motion signals—and the direction of the jump depends on the duration of the inducer. Jump magnitude is robust across jump directions and different types of transient. In addition, when a texture is actually displaced by a large step beyond the upper step size limit of d_{\max} , a breakdown of coherent motion perception is expected; however, in the presence of an inducer, observers again perceive coherent displacements at or just above d_{\max} . In summary, across a large variety of stimuli, we find that when incoherent motion noise is preceded by a small bias, instead of perceiving little or no motion—as suggested by the minimal-motion principle—observers perceive jumps whose amplitude closely follows their own d_{\max} limits.

vision | illusion

Several decades of research on the perception of motion have revealed two fundamental principles—the loss of coherent motion perception above an upper limit and the preference for minimal motion—both of which we challenge here. First, when a random texture is displaced, there is an upper limit, denoted d_{\max} , to the step size that leads to perception of coherent, rigid motion (1–4). Displacements below this limit (whose magnitude may depend on the texture) yield veridical motion percepts, whereas displacements larger than this limit lead to a loss of coherent motion perception. The second principle is that when presented with ambiguous dynamic stimuli, our perception generally corresponds to the slowest motion compatible with the stimulus. This minimal-motion criterion can be observed in the so-called wagon-wheel effect in apparent motion (5), the barber pole illusion in continuous line motion (6), the motion of 2D figures (7), and 3D motion (8). In this article, we present a class of remarkable visual phenomena, which we call “high phi,” that show that both of these assumptions are, at best, incomplete. Truly ambiguous dynamic stimuli and displacements above d_{\max} both lead to maximal motion perception (in a sense described below), coopting the direction of preceding motion signals and greatly amplifying their magnitude. This illusion was independently reported by Ito and Seno (9) and by Wexler (10), and is possibly related to the phenomena reported in ref. 11.

We begin with several basic demonstrations of the high-phi effect (Fig. 1) that illustrate the stimuli used and many of the results obtained in experiments 1–4. In demonstration 1 (the online demonstrations can be found on the Web page <http://lpp.psych.univ-paris5.fr/highphi/>), most observers perceive an annulus undergoing slow and smooth rotations, periodically interrupted by sharp and fast rotatory jumps in the opposite direction. It may therefore come as a surprise that the slow rotations are the only coherent motions in this stimulus. The slow rotations are punctuated by visual transients, which in this case consist of

three successive replacements of the random texture by other, uncorrelated random textures (total duration 50 ms), and which therefore contain no net motion signal corresponding to the fast jumps. Although at first sight this version of high phi may seem to be a motion aftereffect (MAE), it differs greatly from any known version of the MAE. In contrast to the MAE, when viewing a static pattern, the illusory motion here is many times faster than the inducer. [Some stimuli used to study the MAE do lead to large jumps (12–14), but these are imposed by the narrow-band gratings that are used.] There is no known reason why the visual transient should be perceived as coherent motion at all; the fact that it is perceived as very fast motion seems to violate the minimal motion principle. Experiment 1 explores this version of the high-phi effect in more detail.

In a second example of high phi, shown in demonstration 2 and examined in detail in experiment 2, most observers perceive an annulus undergoing fast rotations, alternatively clockwise and counterclockwise, but now seemingly without any preceding motion. The texture actually undergoes a single frame of coherent rotation, by 1° [$\sim 0.1^\circ$ of visual angle (dva)] in alternating directions, followed by two successive random texture replacements. The visual transients mask the actual, small steps; what is perceived is a greatly amplified motion, but one that nevertheless faithfully preserves the unseen, small steps' direction. In demonstration 2, it is possible to remove the transient, leaving only the 1° inducing motion; this removal makes it clear how large the high-phi jump appears to be compared with the actual coherent motion in the stimulus. Notice that the perceived jump is in the opposite direction in demonstration 2 compared with demonstration 1, being backward with respect to the inducing motion in demonstration 1 and forward in demonstration 2. In both cases, it would seem that the visual transient amplifies a preceding motion “seed”: In demonstration 1, the seed arises from motion adaptation, whereas in demonstration 2, the seed is a very small and brief inducing motion.

In a third example, demonstration 3, instead of randomizing texture, we superimpose actual steps on a slow rotation. When these steps are small, their direction—either backward or forward with respect to the preceding slow rotation—is perceived veridically. However, when the step size goes above a certain limit—which we show, in experiment 4, to be closely related to the d_{\max} displacement limit for that particular texture—all steps, either backward or forward, are perceived in the same direction, namely backward with respect to the preceding slow motion. (For very brief preceding motion, as in demonstration 2, all steps are perceived forward.) Moreover, the perceived amplitude of large steps is constant, independent of the actual amplitude of the step and very similar to the high-phi jump obtained with texture

Author contributions: M.W., H.I., and T.S. independently discovered the effect; M.W., A.G., and P.C. designed research; M.W. performed research; M.W. analyzed data; and M.W., A.G., and P.C. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

¹To whom correspondence should be addressed. E-mail: mark.wexler@parisdescartes.fr.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1213997110/-DCSupplemental.

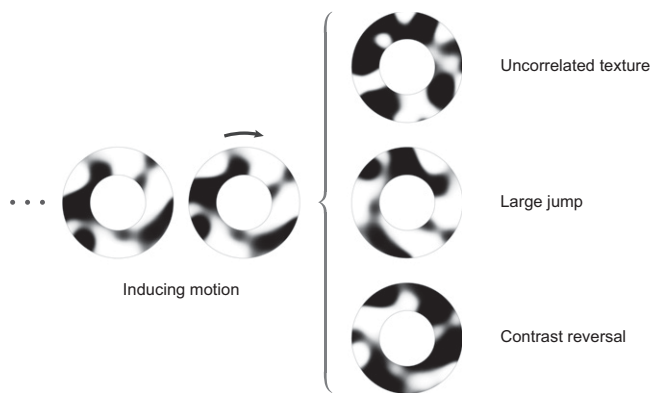


Fig. 1. A schematic illustration of the basic high-phi stimuli. Animated versions may be seen in demonstrations 1–4. During the first phase, the inducer, a random texture is slowly rotated, very briefly or for a longer duration. This inducer is followed by the transient, which may be a replacement of the texture by another, uncorrelated random texture (once or several times); a sudden jump of the original texture by an amount large enough that it cannot be detected; or an inversion of the texture contrast. (Other transients also lead to the effect: see text.) The transient leads to the illusory perception of a very rapid rotation, either forward (with respect to the direction of the inducer)—provided the inducer is very brief—or backward—for longer inducers.

randomization. Thus, motion perception does not break down when steps go above the d_{\max} limit but becomes stereotyped in both amplitude and direction. In effect, as we show below, in this regime observers perceive jumps whose amplitude closely follows their own d_{\max} limits.

The stimuli drawn schematically in Fig. 1 show some basic elements of the high-phi phenomenon. A random texture undergoes first-order motion due to correspondence between frames. This inducing motion can be long, as in demonstrations 1 and 3, or very brief, as in demonstration 2. The motion shown in Fig. 1 and studied in the rest of this article is rotation, but other types of motion—such as linear translation, shear, and expansion and contraction—also lead to similar effects. The inducing motion is followed by a visual transient, which may be of several types. As we have already shown, the sudden replacement of the texture by a different, globally uncorrelated random texture induces the perceived high-phi jump (demonstrations 1 and 2), and large steps above the displacement limit (demonstration 3). Other transients that induce high phi are contrast reversals, or showing the inducing motion to one eye and suddenly transferring the stimulus to the other eye. Some of the transients may be compared in demonstration 4 (experiment 3), in which most observers perceive very similar jumps despite the different transient types. None of the transients have any detectable net motion signals; locally, however, the transients induce many accidental matches, flooding local motion detectors with incoherent, broadband energy. We propose that when combined with the preceding motion seed, this non-directional energy takes on the direction of the seed but now specifies a much larger jump, consistent with the high level of energy but constrained by the maximum jump size that can be registered, d_{\max} .

Results

In experiment 1, we measured the properties of the high-phi jump and its dependence on several stimulus factors, using direct report. This measurement was possible because of high within-observer, intertrial consistency, which can be observed by subjectively comparing amplitudes of successive jumps in demonstration 1 or 2. Observers watched a randomly textured annulus that first rotated and then underwent texture randomization. In a factorial design, we varied the length of the randomization

transient (from one to seven frames, 17–117 ms), the spatial frequency content of the textures (low-pass filtered noise with cutoff frequencies from 0.47 to 11.7 cycles per dva), and the speed of initial rotation (from 10° to 30° of rotation per second, corresponding to ~1–3 dva per second). After the stimulus disappeared, observers reported the direction and amplitude of the perceived jumps using a visual probe controlled by a knob.

We found that in 94% of the trials, observers reported a backward jump (with respect to the preceding motion), with a mean amplitude of ~67° of rotation. The detailed dependence of the perceived jump on the stimulus parameters is shown in Fig. 2. As can be seen in Fig. 2*A* (and readily experienced in demonstration 5), the jump amplitude increased with the duration of the transient: Mean jump amplitude was 37° for a one-frame transient, but increased to 80° for a seven-frame transient. Indeed, a duration \times frequency \times speed ANOVA showed that the main effect of transient duration was significant ($P < 0.0001$). Fig. 2*B* shows the effect of spatial frequency, which can be experienced in demonstrations 6 and 7: Jump amplitude increased with decreasing spatial frequency. Mean amplitude was 41° for the highest frequencies and 71° for the lowest. The main effect of spatial frequency was also significant ($P < 0.0001$). The interaction of transient duration and spatial frequency, which was also significant ($P < 0.0001$), is shown in Fig. 2*C*: The slopes of jump amplitude as a function of transient duration increased with decreasing spatial frequency. None of the other effects or interactions was significant. In particular, as shown in Fig. 2*D*, over a range of a factor of 3, inducer speed had no effect on the jump (demonstration 8).

What is the perceived speed of the high-phi jump? As a first approximation, we can compute how the reported jump angle increases with the transient duration—in other words, the slope of the curves in Fig. 2*A* and *C*. The mean regression slope is 429° of rotation, with large variations between observers: the lowest observer has a speed of 179°/s and the fastest a speed of 730°/s. It should be noted that, on average, these speeds are >20 times the speed of the inducing stimulus. These computed speeds are not necessarily the perceived speeds (perceived duration may not equal physical duration, and perceived speed may not be perceived displacement divided by perceived duration), but are probably reasonable approximations.

In experiment 2, we studied the transition between jumps that are backward with respect to the inducing motion, and those that are forward. As discussed in the introductory paragraphs, the direction of the jump depends on the duration of the inducing motion: long inducers lead to backward jumps (with respect to the direction of the inducer), whereas brief inducers lead to forward jumps—as can be observed in demonstration 9. In experiment 2, we systematically varied the duration of the inducer preceding a single random texture replacement, while asking participants to report the perceived jump direction. All transients were followed by 600 ms of motion at the same velocity as the inducer. We also varied the spatial frequency of the stimulus and inducer speed. The results for individual subjects and pooled over all stimulus frequencies and inducer speeds are shown in Fig. 3. For small nonzero inducer durations, all participants perceived forward jumps most often. For longer inducers, perceived jump direction reversed. When there was no inducer preceding the transient (but there was always motion following the transient), responses were random, showing that motion preceding, but not following, the transient determines the direction of the jump.

To quantitatively estimate the inducer duration at which the transition between forward and backward jumps takes place, we fitted the data in Fig. 3 using cumulative Weibull distributions. For all frequencies and speeds pooled together, the mean transition was at 110 ms, averaged over participants. We also found that the transition duration increased significantly as spatial frequency decreased (mean transition 82 ms for the highest

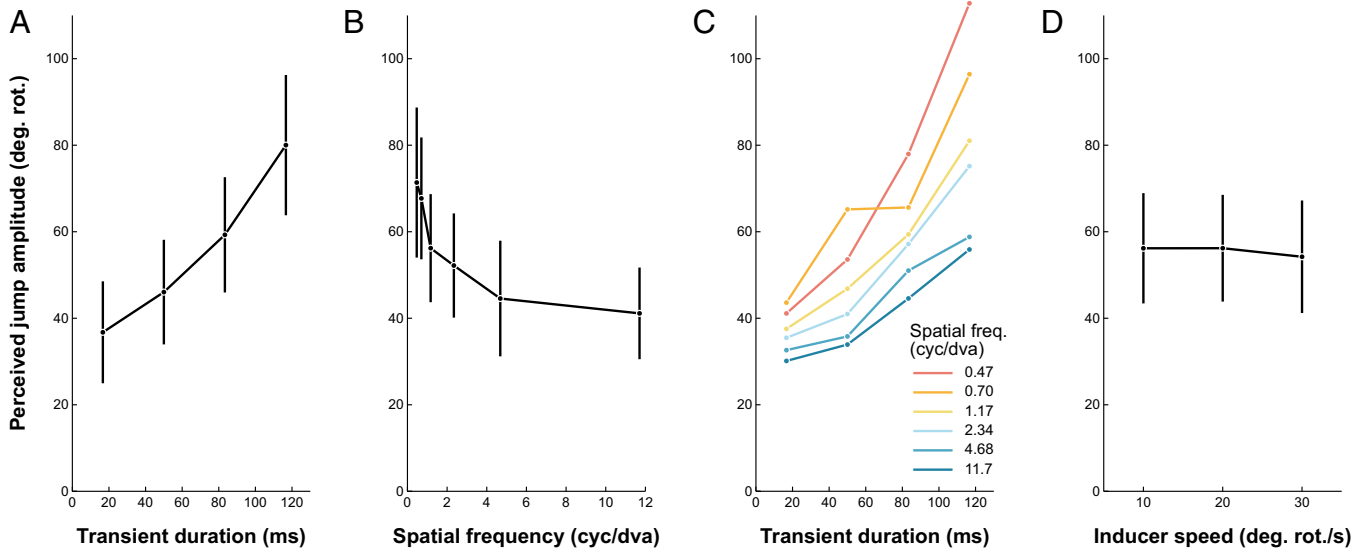


Fig. 2. Dependence of the high-phi jump on the duration of the transient, spatial frequency, and inducer speed (all data are from experiment 1). In all graphs, the y axis shows mean reported jump angle in degrees of rotation, with positive angles denoting directions opposite to that of the inducing motion. Error bars denote between-subject 95% confidence intervals. (A) Effect of transient duration. (B) Effect of stimulus spatial frequency (cutoff frequency of low-pass filter, cycles per dva). (C) Interaction between transient duration and spatial frequency: mean jump as a function of transient duration, for different spatial frequencies. (D) No effect of inducer speed (degrees of rotation per second).

frequency, 166 ms for the lowest; $P < 0.0001$; ANOVA), and as inducer speed increased (transition duration 104 ms for lowest speed, 126 ms for highest; $P = 0.04$).

In experiment 3, we investigated the unity of different high-phi phenomena by using within-subject correlations. We have seen

that by varying the duration of the inducing motion, we can obtain either backward jumps with long inducers or forward jumps with brief inducers. Are these two types of jump a unitary phenomenon or two separate effects? As we have seen in experiment 1, there are significant variations across subjects in the amplitude of the perceived jump. In experiment 3, we used these variations to study whether the two types of jumps are related. If they are, then participants who perceive small jumps in one condition should also perceive small jumps in the other, and the same should be true for large jumps. We therefore measured within-subject correlations of perceived jump amplitudes with very brief (“brief-random”) and long (“long-random”) inducers, using one-frame texture randomization transients. Fig. S1A shows the within-subject correlation in amplitudes of these two types of jump. The correlation was excellent ($R^2 = 0.966$) and statistically significant ($P < 0.0001$); the regression slope, 1.02, did not differ significantly from 1.

Experiment 3 included another type of transient, texture contrast reversal, that leads to a high-phi jump—as can be seen in demonstration 4. We included a “long-negative” condition, similar to the long-random condition, except that the transient was generated by a single contrast reversal. The results for within-subject amplitude correlations with the two texture-randomization conditions, brief- and long-random, are shown in Fig. S1 B and C. Both correlations were significant, with slopes that did not differ significantly from 1.

Experiment 3 included a final stimulus, in which a small texture rotation and contrast reversal occurred simultaneously, known as reverse-phi motion. This stimulus typically leads to perception of motion in the opposite direction to that of the step (15, 16). Apart from very-narrow-band stimuli, the mechanisms of reverse-phi motion are imperfectly understood. In high phi with a brief inducer, a texture moves over one or a small number of frames and then undergoes a transient, such as contrast reversal; in reverse phi, the motion and contrast reversal occur simultaneously (demonstration 10). The within-subject amplitude correlations, shown in Fig. S1 D–F, are once again excellent, with all three correlations significant, and all slopes not significantly different from 1.

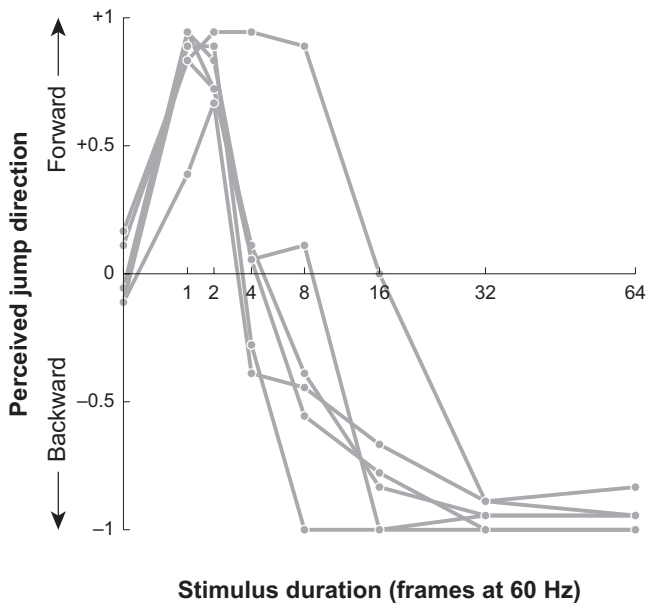


Fig. 3. Dependence of the direction of the high-phi jump on the duration of the inducer (experiment 2). The x axis (nonlinear scale for better visibility) shows the duration of the inducer, in monitor frames, with the duration of each frame equal to 1/60 s. The y axis shows mean reported direction, with +1 denoting the same direction as the inducer and –1 denoting the opposite direction. Shown are individual data for the six participants, pooled over all frequencies and speeds. Responses (excluding duration 0) were fitted by using cumulative Weibull distributions to calculate the duration at the transition between backward and forward jumps. Mean transition duration was 110 ms, ranging from 59 to 267 ms in individual data.

However, it might be argued that the correlations found in experiment 3 could simply arise from participants' consistent response bias for reporting smaller or larger jumps across all conditions. As in experiment 1, we found that changes in spatial frequency led to wide variation in perceived jump size. We therefore also performed a linear regression of perceived jump amplitude vs. spatial frequency and found that the slopes of these regressions were also correlated across subjects in all six pairs of conditions. All R^2 values were >0.7 , and all correlations were significant, showing that response bias could not explain the correlations. In summary, we have demonstrated several types of detailed, within-subject correlations between reported jump amplitudes and their dependence on spatial frequency—showing that the three versions of high phi as well as reverse phi are likely to be a unitary phenomenon, independent of the details of the inducer or the transient.

In experiment 4, we examined the connections between high phi and the perception of real steps. As discussed in the *Introduction*, a way to induce high-phi jumps is by suddenly rotating textures beyond a certain limit in the presence of an inducing motion, such as a long, slow rotation (as can be seen in demonstration 3). (For brevity, we will use “forward” or “backward” to refer to rotation directions in the same or opposite direction to the preceding or inducing motion.) Small steps are generally perceived veridically, at least as concerns their direction. Beyond a certain range, however, all steps, forward or backward and of whatever amplitude, are perceived as jumps with a roughly fixed amplitude and with a direction that depends on the inducer; for a long inducer, as here, large steps are perceived as backward. In experiment 4, we superimposed real steps on a slowly rotating textured ring, and participants reported the perceived direction and amplitude of the steps.

Data for individual participants are shown in Fig. 4, with forward steps shown as positive and backward ones shown as

negative. For each participant, there is a region around 0° of rotation where the perceived step is roughly a linear function of the real step. Outside of this range, both for forward jumps (on the right) and backward jumps (on the left), there is a plateau in which all steps are perceived as backward jumps, with a roughly uniform amplitude—we will call this the “plateau jump.” To compare this plateau jump to the previously studied forms of the high-phi effect, we also included trials in which, instead of a step, the texture underwent a random replacement. Perceived jumps for these trials are shown by green dots in Fig. 4. Their mean values, shown by the large green dots in Fig. 4, appear to be closely related to the plateau jumps.

We fitted the data from the real step trials to a piecewise-linear model with three parameters: steps with absolute value below a cutoff (first parameter) are veridically perceived, but with amplitude multiplied by a gain factor (second parameter), and above the cutoff all steps are perceived as a constant plateau jump (third parameter). The fitted models for each participant's data are shown in red in Fig. 4. For trials with step sizes below the cutoff, we found that the direction of the step was reported correctly in 96% of all trials (but with a mean gain of 1.87); for steps above the cutoff, the reported direction was correct in only 56% of all trials. The cutoff—the maximum step at which step direction can be reliably reported—is nothing other than d_{\max} (and which we express in degrees of rotation rather than the usual dva).

The three arrows shown for one participant in Fig. 4 highlight some important aspects of the data. The vertical black arrow shows the cutoff or d_{\max} . The upper horizontal arrow (blue) shows the perceived jump size at d_{\max} —the amplitude that the subject reports for the largest step size at which the direction can still be reliably reported. The lower horizontal arrow (purple) shows the perceived plateau jump. It is interesting to note that

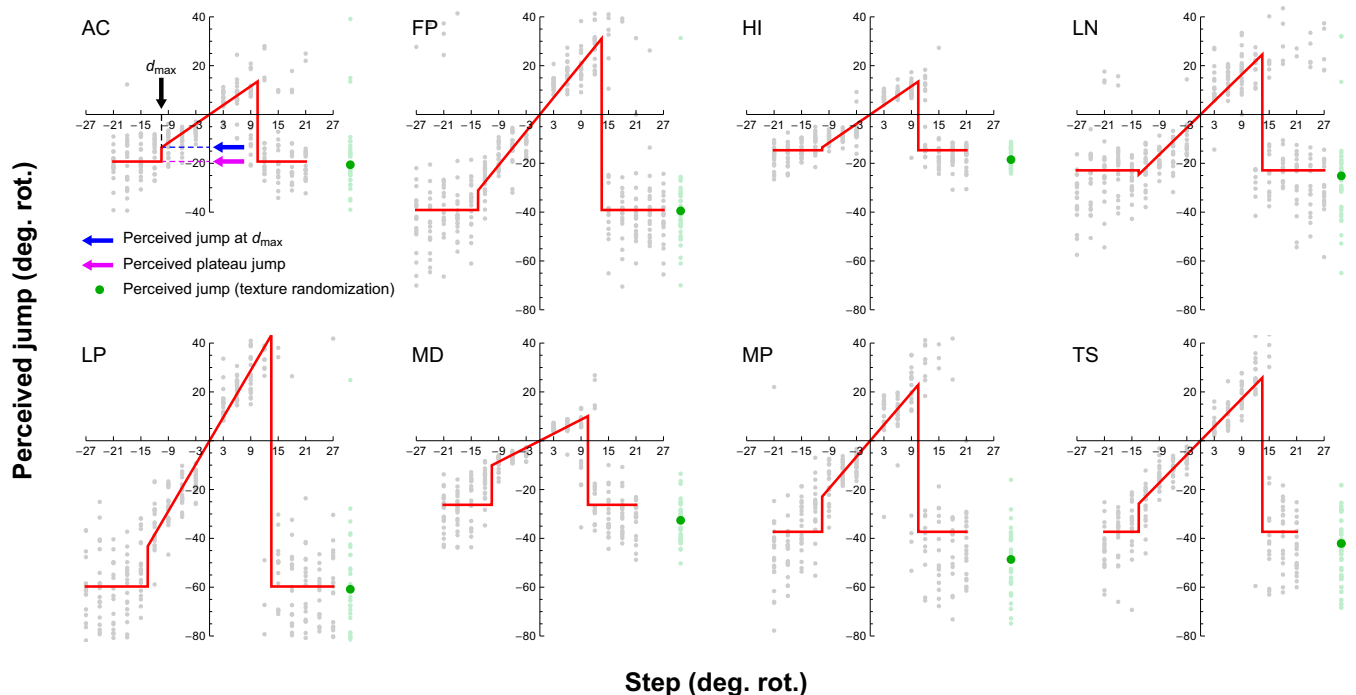


Fig. 4. Perceived steps as a function of actual steps, in degrees of rotation (experiment 4). Steps were superimposed on slow rotations. Steps in the same direction as the slow rotation are represented here as positive (we call these forward); steps in the opposite direction are negative (backward). Data are shown for the eight individual participants, with each gray point representing one trial. Light green dots on the right show trials on which, instead of the real step, the texture was randomized on one frame; the large green dot shows the mean perceived jump on these trials. The red curve shows the piecewise-linear fits described in the text. The vertical black arrow shows the cutoff or d_{\max} for one participant. The upper horizontal arrow (blue) shows the perceived jump size at d_{\max} . The lower arrow (purple) shows the perceived plateau jump.

these last two measures seem to be closely related: The plateau jump was usually close to, but slightly larger than, perceived jump at cutoff. To explore this relationship, we performed a linear regression of the former vs. the latter across participants and found a significant correlation ($P = 0.003$) with $R^2 = 0.79$ and a slope of 1.17. Finally, we performed a linear regression of the mean perceived jump on the randomization trials against the perceived step at cutoff and found a significant correlation ($P = 0.004$) with $R^2 = 0.78$, and a slope of 1.03.

Thus, we have shown an interesting pattern in the perception of real steps superimposed on slow rotations. With amplitudes below a cutoff, steps are perceived approximately veridically; above this cutoff, all steps are perceived as a large, default jump. This default jump is the same phenomenon as the standard high-phi jump, obtained with texture randomization or other transients and studied in the previous three experiments. Most importantly, the default jump is closely correlated with, and on average just slightly greater than, the largest veridically perceived step. In other words, when seeing the high-phi jumps, observers perceive jumps that closely correlated to their own d_{\max} and that are on average slightly above their d_{\max} values. However, we should not make much of the finding that jumps are above d_{\max} ; if we had defined the cutoff threshold less conservatively, we would have obtained higher values for d_{\max} .

Discussion

We have found that motion transients that contain no detectable net motion signals are perceived as coherent jumps at or just above the d_{\max} limit, when in the presence of a directional motion inducer. In the first experiment, we showed that for long-duration inducers (several seconds), high-phi jumps are backward with respect to the inducing motion and have amplitudes that increase with transient duration, decrease with increasing spatial frequency, and do not depend on inducer speed. In the second experiment, we showed that the direction of the jump depends on the duration of the inducer, with brief inducers leading to forward jumps and longer inducers to backward jumps. In a third experiment, we showed that high phi is a unitary phenomenon, invariant across different inducers and different transients, and that it is closely related to reverse-phi motion. Finally, a fourth experiment showed that real steps, above a certain threshold, are perceived as high-phi jumps and that this amplitude is just above that of the largest veridically perceivable step.

The most surprising aspect of the high-phi phenomena is the magnitude of the jump, which seems to contradict accepted ideas about the minimal-motion criterion and motion breakdown above d_{\max} , the largest discriminable motion step. Several of our results point to the close relationship between the high-phi jump and d_{\max} . Experiment 1 showed that high-phi jumps increase as spatial frequency decreases, as does d_{\max} (3), rising slowly at high frequencies and faster at lower frequencies, as does d_{\max} (17). We have found that high phi increases with duration, again a characteristic of d_{\max} (18). More directly, experiment 4 showed that high-phi amplitudes, although quite variable across subjects, are closely correlated to subjects' d_{\max} values and that the dependencies of the two variables on spatial frequency are also correlated across subjects. In particular, high-phi amplitudes are at or just above individuals' d_{\max} .

It might be thought that high phi is the result of a motion prediction or extrapolation mechanism, with the transient playing the role of the flash in the flash-lag effect, for instance (19). However, the lack of any dependence of the amplitude on the inducer speed, as found in experiment 1, makes this hypothesis unlikely. Another possible explanation might involve the integration of motion signals over an extended period, such as a low-pass filter (20). Low-pass filtering can extend a motion response in time, but because it is essentially averaging, it cannot amplify motion response to produce the large jumps that we

observe, nor would it predict the close correlation with d_{\max} over a wide range of conditions. Experiment 3 showed that several very different types of inducers and transients lead to the very same perceived jump, and the null effect of inducer speed in experiment 1 also seems to argue against a temporal filtering explanation. All other effects on high phi that we have found, such as that of spatial frequency, match the effects of these variables on d_{\max} .

From a global viewpoint, the texture after the transient has near-zero correlation with the texture before the transient (in the case of random replacement) or has a correlation at an inaccessible step size (for large steps). (Because of temporal filtering, the texture change will actually be smeared over time, so correlation between pre- and posttransient textures only approaches zero after a finite time interval. However, this smearing has no bearing on our argument, because the texture change, independently of the degree of temporal filtering, carries no net motion energy.) It may be thought that the visual system first excludes globally coherent correspondences, arising from rigid motions of the stimulus, up to a magnitude of d_{\max} . Because none of the steps outside this range (above d_{\max}) have been excluded, all are equally compatible with the sensory data. An application of the minimal-motion principle would then fix the step size just above this excluded range. Paradoxically, such an application of the minimal-motion principle would yield perception of a very large and illusory motion. Thus, sensory data may be used negatively, to exclude a range of steps, rather than positively, to locate a given step. We might call such a computation an exclusion mechanism.

Local motion detectors, however, will be sensitive to accidental correspondences, occurring at all scales and in all directions during the transient. In this sense, the motion-detection system is flooded by the broadband transients. However, why does this incoherent correspondence noise lead to the perception of coherent motion at all, and moreover of maximally large steps? The motion energy from the displacement of a random texture scales with step size up to a maximum at the largest step size supported for the texture, d_{\max} . When a stimulus produces more motion energy than can be explained by any steps smaller than d_{\max} but still has a directional bias (from the seed), then the perceived step size defaults to d_{\max} or slightly above. Thus, the d_{\max} limit of a texture must be available to the visual system, even in the absence of a real step. This availability is required by the fact that in our high-phi stimulus with texture randomization or contrast reversal transients, there is no actual displacement, and yet observers perceive a step size that corresponds to what d_{\max} would be if there had been a real step. There may be many reasons why it would be advantageous for the visual system to estimate the range of motion steps that are compatible with a given texture, including a greater sensitivity for steps within a detectable range. Whatever the reason, it is remarkable that motion perception is constrained by d_{\max} , even in the absence of real, coherent motion.

If the above arguments lay out possible causes for large magnitude of the high-phi jump, they do not explain its direction. In a possibly related effect, when motion direction is axially constrained using Glass patterns in dynamic noise, fast motion is seen oriented along the axis, but with arbitrary sign (21). For all of the data here, the direction of the large jump can be predicted by integrating the small motion signals present at the onset of the transient, over a brief temporal window preceding it—giving the same direction as the inducer for brief inducing motion, but the opposite, the direction of the MAE, for longer inducers. The time course is very similar to that found for the perceived direction of motion adaptation—motion priming for brief inducers but an aftereffect for longer inducers (22–24). What is truly surprising is that the directions of these tiny motion signals are somehow attributed to the huge jumps. For example, a 0.3° of rotation step immediately followed by a transient can power a 30° high-phi jump in many observers—which will almost always be perceived in the same direction as the 0.3° step. The subsequent transient has

motion energy at all scales and, symmetrically, in all directions. How the tiny preceding motion signals break this symmetry, with motion direction on the smallest scales being attributed to motion on the largest scales, in what can only be a nonlinear interaction, remains unknown. Although motion detectors encode both speed and direction of motion (25, 26), the attribution of the inducer's direction to the directionally ambiguous high-speed neural representation may be a case of misbinding of visual attributes (27, 28).

Methods

In all experiments, stimuli consisted of rotating rings filled with random textures. The rings had an inner radius of 4 dva and an outer radius of 8 dva; there was a small dot in the empty center of the ring on which participants were instructed to fixate. Textures were generated by applying low-pass filters to random pixels. In experiment 1, we used a rectangular filter with one of six bandwidths: 0.47, 0.70, 1.17, 2.34, 4.68, and 11.7 cycles per dva; in experiments 2 and 3, we used a Gaussian filter with 3-dB bandwidths of 0.31, 0.62, and 1.24 cycles per dva; in experiment 4, we used a Gaussian filter with 3-dB bandwidth of 0.31 cycles per dva. Textures were normalized to equalize all means and variances. Stimuli were displayed on a cathode ray tube monitor (Sony; GDM F520; resolution 1,280 × 960, pixel size 1.8 arcmin of visual angle, refresh rate 60 Hz), which, other than the textured ring and fixation point, was filled with the mean gray value of the texture. Participants sat ~57 cm from the monitor in a darkened room, with their head stabilized by a chinrest.

Following the presentation and disappearance of the stimulus, the participants' task was to indicate both the direction, clockwise or counterclockwise, and the angular amplitude of the perceived jump (experiments 1, 3, and 4) or only the direction (experiment 2). Responses were given by using a knob placed horizontally on a table, to which participants could apply small twists about a vertical axis (SpaceMouse Pro; 3Dconnexion). When reporting both perceived direction and amplitude, a visual probe was displayed on the monitor, consisting of two arrows that traced circular arcs at the mean eccentricity of the stimulus ring; participants adjusted the angle and direction of the arrows by twisting the knob to match the direction and angular amplitude of the perceived jump. When reporting only direction, the response was given by the direction of the twist.

In experiment 1, stimuli rotated in either direction at 10°, 20°, or 30°/s for a randomly chosen duration between 3 and 5 s. (When speaking about speeds or angular displacements of our stimulus, we use degrees of rotation, not to be confused with dva. With an annulus having a mean radius of 6 dva, 1° of rotation corresponds to ~0.1 dva.) This inducing phase was followed by

a transient, which consisted of one, three, five, or seven monitor frames (17–117 ms), with a new, uncorrelated texture being presented on each frame. Following the transient, the final texture rotated at the same angular velocity as the inducer and was visible for 600 ms, gradually fading during the last 200 ms. In experiment 2, the inducer was first shown motionless for 1 s, then rotated at 10 or 30°/s for 0, 1, 2, 4, 8, 16, 32, or 64 monitor frames (0–1.067 s). The inducer was followed by a one-frame transient (i.e., the replacement of the original texture by a new texture), which rotated in the same direction as the inducer for 600 ms, as in experiment 1.

In experiment 3, there were four conditions: long-random, long-negative, brief-random, and reverse phi. The long-random condition was similar to experiment 1, with a one-frame transient consisting of texture randomization and 1–2.5 s of inducing motion at 20° of rotation per second. The long-negative condition was identical to long-random, except that the transient consisted of reversing texture contrast. The brief-random condition was like long-random, except that the texture only rotated for two frames, by 0.5° on each frame, before the randomization transient. Finally, in the reverse-phi condition, the texture simultaneously rotated by 2° and underwent texture contrast reversal on one frame. In all conditions, following the transient, the texture continued to rotate for 400 ms, fading out during the last 200 ms.

Experiment 4 had two conditions, real steps and randomization. Stimuli were shown motionless for 0.5 s, then rotated at 20°/s for 1 s. In the real-step condition, the stimulus stopped for 100 ms, then stepped on a single frame by 3°, 6°, 9°, 12°, 15°, 18°, or 21° of rotation (and additionally, for some participants, by 24° and 27°), either forward or backward with respect to the preceding motion, and without change in texture. (The 100-ms pause was found in pilot studies to help subjects to segregate small steps from inducing motion, without altering the main effects.) Following the step, the texture continued to rotate for 400 ms, fading out during the last 200 ms. The randomization condition was identical, except that instead of the step, the old texture was replaced by a new, uncorrelated one.

The number of participants was nine, six, nine, and eight in experiments 1–4, respectively, with all participants naive except two in each of experiments 2–4. All participants had normal or corrected-to-normal vision. All participants gave informed consent, and were treated in accordance with the relevant provisions of the Declaration of Helsinki.

ACKNOWLEDGMENTS. We thank Thérèse Collins, Frans Verstraten, Katsumi Watanabe, Srimant Tripathy, Rick Born, and George Mather for stimulating conversations; and Marianne Duyck and Hanako Ikeda for help in running the experiments. This research was partially supported by European Research Council Advanced Grant PATCH and the Wellcome Trust.

- Braddick O (1974) A short-range process in apparent motion. *Vision Res* 14(7):519–527.
- Lappin JS, Bell HH (1972) Perceptual differentiation of sequential visual patterns. *Percept Psychophys* 12:129–134.
- Chang JJ, Julesz B (1983) Displacement limits for spatial frequency filtered random-dot cinematograms in apparent motion. *Vision Res* 23(12):1379–1385.
- Nakayama K, Silverman GH (1984) Temporal and spatial characteristics of the upper displacement limit for motion in random dots. *Vision Res* 24(4):293–299.
- Ullman S (1979) *The Interpretation of Visual Motion* (MIT Press, Cambridge, MA).
- Wallach H Ueber visuell wahrgenommene Bewegungsrichtung. *Psychol Forsch* 20:325–380. German.
- Weiss Y, Simoncelli EP, Adelson EH (2002) Motion illusions as optimal percepts. *Nat Neurosci* 5(6):598–604.
- Wexler M, Panerai F, Lamouret I, Droulez J (2001) Self-motion and the perception of stationary objects. *Nature* 409(6816):85–88.
- Ito H, Seno T (2009) Reversed motion perception during blinks. *Perception* 38:90.
- Wexler M (2011) An ultra-fast motion aftereffect. *J Vis* 11(11):756.
- Green M, Chilcoat M, Stromeyer CF, 3rd (1983) Rapid motion aftereffect seen within uniform flickering test fields. *Nature* 304(5921):61–62.
- von Grünau MW (1986) A motion aftereffect for long-range stroboscopic apparent motion. *Percept Psychophys* 40(1):31–38.
- von Grünau MW, Dubé S (1992) Comparing local and remote motion aftereffects. *Spat Vis* 6(4):303–314.
- Nishida S, Sato T (1995) Motion aftereffect with flickering test patterns reveals higher stages of motion processing. *Vision Res* 35(4):477–490.
- Reichardt W (1961) Autocorrelation, a principle for the evaluation of sensory information by the central nervous system. *Sensory Communication*, ed Rosenblith WA (Wiley, New York), pp 303–317.
- Anstis SM (1970) Phi movement as a subtraction process. *Vision Res* 10(12):1411–1430.
- Morgan MJ (1992) Spatial filtering precedes motion detection. *Nature* 355(6358):344–346.
- Ramachandran VS, Anstis SM (1983) Displacement thresholds for coherent apparent motion in random dot-patterns. *Vision Res* 23(12):1719–1724.
- Nijhawan R (1994) Motion extrapolation in catching. *Nature* 370(6487):256–257.
- Nakayama K (1985) Biological image motion processing: A review. *Vision Res* 25(5):625–660.
- Ross J, Badcock DR, Hayes A (2000) Coherent global motion in the absence of coherent velocity signals. *Curr Biol* 10(11):679–682.
- Pinkus A, Pantle A (1997) Probing visual motion signals with a priming paradigm. *Vision Res* 37(5):541–552.
- Kanai R, Verstraten FAJ (2005) Perceptual manifestations of fast neural plasticity: Motion priming, rapid motion aftereffect and perceptual sensitization. *Vision Res* 45(25–26):3109–3116.
- Priebe NJ, Churchland MM, Lisberger SG (2002) Constraints on the source of short-term motion adaptation in macaque area MT. I. The role of input and intrinsic mechanisms. *J Neurophysiol* 88(1):354–369.
- Maunsell JHR, Van Essen DC (1983) Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed, and orientation. *J Neurophysiol* 49(5):1127–1147.
- Perrone JA, Thiele A (2001) Speed skills: Measuring the visual speed analyzing properties of primate MT neurons. *Nat Neurosci* 4(5):526–532.
- Moutoussis K, Zeki S (1997) A direct demonstration of perceptual asynchrony in vision. *Proc Roy Soc Lond B Bio* 264(1380):393–399.
- Nishida S, Johnston A (2002) Marker correspondence, not processing latency, determines temporal binding of visual attributes. *Curr Biol* 12(5):359–368.