

OBSERVATION

Visual Perception of Apparent Motion Abides by Minimization Principles of Geometry

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Apparent motion is a robust perceptual phenomenon in which observers perceive a stimulus traversing the vacant visual space between two flashed stimuli. Although it is known that the “filling-in” of apparent motion favors the simplest and most economical path, the interpolative computations remain poorly understood. Here, we tested whether the perception of apparent motion is best characterized by Newtonian physics or kinematic geometry. Participants completed a target detection task while Pacmen-shaped objects were presented in succession to create the perception of apparent motion. We found that target detection was impaired when apparent motion, as predicted by kinematic geometry, not Newtonian physics, obstructed the target’s location. Our findings shed light on the computations employed by the visual system, suggesting specifically that the “filling-in” perception of apparent motion may be dominated by kinematic geometry, not Newtonian physics.

Public Significance Statement

There is much agreement that perception is a constructive process, yet the mechanisms that underlie this process are debated. In an effort to add to this important literature, the present study distinguished between two viable principles of apparent motion perception: Newtonian physics versus kinematic geometry. In apparent motion, individuals interpolate (i.e., “fill in”) motion between 2 sequentially presented objects, but the principles of interpolation in this paradigmatic case of constructive perception remain elusive. Using an implicit measure of apparent motion, we found that participants perceived a path of motion that favored the shortest trajectory, as predicted by kinematic geometry, not the least cost of energy, as predicted by Newtonian physics. This research adds to our understanding of the constructive processes implicated in visual perception.

Keywords: vision, perception, apparent motion, Gestalt, geometry

A hallmark of visual perception is interpolation. The visual system “fills in” information to maintain a robust perception of the physical world. In a world where motion is ubiquitous, human vision has evolved to favor the most economical paths of motion (Restle, 1979; Wagemans et al., 2012). For example, when an object on a straight-line trajectory travels behind an occluder, observers interpolate a path of motion that is consistent with the original straight path, not one

that deviates from it (e.g., a circular trajectory). As a legacy from Gestalt theory, this simplicity heuristic is referred to as the minimum principle. Yet the interpolative computations that underlie minimization remain poorly understood.

One possibility for implementing minimization within the visual system is via Newtonian physics. According to Newtonian physics, the minimum principle follows the principle of least action (Hanc & Taylor, 2004), such that there is a minimization of overall energy expenditures (Buckley et al., 2017; Mousavi & Sunder, 2019). Mach (1914) claimed that the principle of least action was adopted by human perception, in line with the likelihood principle (Chater, 1996), wherein perception finds the most likely organization consistent with the sensory input. Accumulating research suggests that causal events are perceived according to Newtonian principles such as force and mass distribution (Battaglia et al., 2013; Bramley et al., 2018; Deeb et al., 2021; Hamrick et al., 2016; Hecht & Bertamini, 2000).

Kinematic geometry, however, accounts for motion via geometric properties, without considering mass or force (Carlton & Shepard, 1990a). The essence of kinematic geometry is geodesic in

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All data, including those in supplemental experiments, have been made available on OSF (<https://osf.io/xkm9y/>).

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nature, such that it is concerned with the mathematically shortest distance between points. Evidence from neuroimaging demonstrates that brain regions involved in visual motion processing show activation characterized by geometric invariants (Dayan et al., 2007). Moreover, developmental studies with human infants demonstrate an early sensitivity to geometric properties, such as relative length and angle (Lourenco & Huttenlocher, 2008; Schwartz & Day, 1979; Slater & Morison, 1985), which contrasts with a relatively late-developing sensitivity to forces (Kim & Spelke, 1999; Spelke et al., 1994).

Although the extant research suggests that visual perception is sensitive to both Newtonian physics and kinematic geometry, few studies have directly dissociated the two principles when characterizing the perception of motion. The difficulty in conducting such research may be due, in large part, to the fact that Newtonian physics and kinematic geometry are not straightforwardly differentiated in the physical world, where forces often act on physical objects. Apparent motion, however, is a closed system without real forces, relying on the mental construction of motion and, thereby, representing a unique case in which to dissociate the two computations.

There has been much research on the phenomenon of apparent motion (Bermeitinger, 2013; Foster, 1978; Hecht & Proffitt, 1991; Werkhoven et al., 1990; Yantis & Nakama, 1998), including the neural mechanisms (Chong et al., 2016; Tse, 2006), but the question of whether its perception abides by Newtonian physics or kinematic geometry has received less attention. A rare example is the study of McBeath and Shepard (1989), in which participants were tasked with making an explicit judgment about the position of a gap to allow for the inferred path of motion between two objects presented sequentially at different orientations. Participants judged the path of motion as curved, as predicted by kinematics, not a straight path, as predicted by Newtonian physics (for replication, see OSF). Shepard and colleagues (Carlton & Shepard, 1990b; Shepard, 1994, 2001) argued that kinematic geometry is internalized by the visual system (but see Prakash et al., 2020; Todorovič, 2001). However, because the task required the manual adjustment of a vertical gap, it is unknown whether the visual system per se abides by kinematic geometry, or whether the results reflect simulation and interpretation by the action system, specifically motor planning, or other higher-level, strategic processes such as mental rotation, in which the movements of an object may undergo rigid transformations (Sanders et al., 2014; Searle & Hamm, 2017; Shepard & Judd, 1976). Indeed, evidence from a static version of this task, in which two objects were presented simultaneously (no apparent motion), demonstrated that participants predicted movement consistent with kinematics, as would be expected if participants engaged in mental rotation (for data, see OSF).

Using a masking procedure, we provide a novel test of whether apparent motion perception abides by Newtonian physics or kinematic geometry. We adapted the paradigm of Yantis and Nakama (1998), in which apparent motion interfered with target detection of an object along the path of movement. Two circles were presented in alternation, resulting in translational movement along a single axis. When tasked with detecting a target, participants showed longer reaction times (RTs) when the target was positioned along the path of perceived motion compared to when it was off this path. In the present study, we presented Pacmen-

shaped stimuli at different angles, as in McBeath and Shepard (1989), to permit paths of apparent motion consistent with either Newtonian physics or kinematic geometry.

The current approach provides a strong test of the constraints of visual perception independent of higher-level processing because no explicit judgment about apparent motion is required. Instead, the dependent variable is RT related to target detection—with an orthogonal path of perceived motion interfering with target detection along this path and resulting in longer RTs. Moreover, it has been suggested that the interference effect on target detection is instantiated in early visual cortex (EVC), including V1 (Hidaka et al., 2011; Muckli et al., 2005), such that EVC activity is suppressed when the target overlaps with the path of apparent motion (Shen et al., 2020). Thus, interference on target detection caused by apparent motion can be interpreted as an effect of visual perception per se.

Method

Participants

Forty-three undergraduates participated for course credit ($M = 18.5$ years, 15 males). Sample size was determined a priori using a power analysis conducted in BUCSS R package (Anderson et al. [2017] Version 1.2.1). Of interest here was a within-subject effect of target position, as determined by either Newtonian physics or kinematic geometry (alpha level = .05, power = .8, assurance level = .5; effect size [$d = 2.9$] based on Yantis & Nakama [1998]). Correcting for uncertainty and publication bias, the power analysis indicated a minimum sample size of 42 participants for paired-samples *t*-tests.¹

All participants had normal or corrected-to-normal vision, and all provided written informed consent. Experimental procedures were approved by the university IRB.

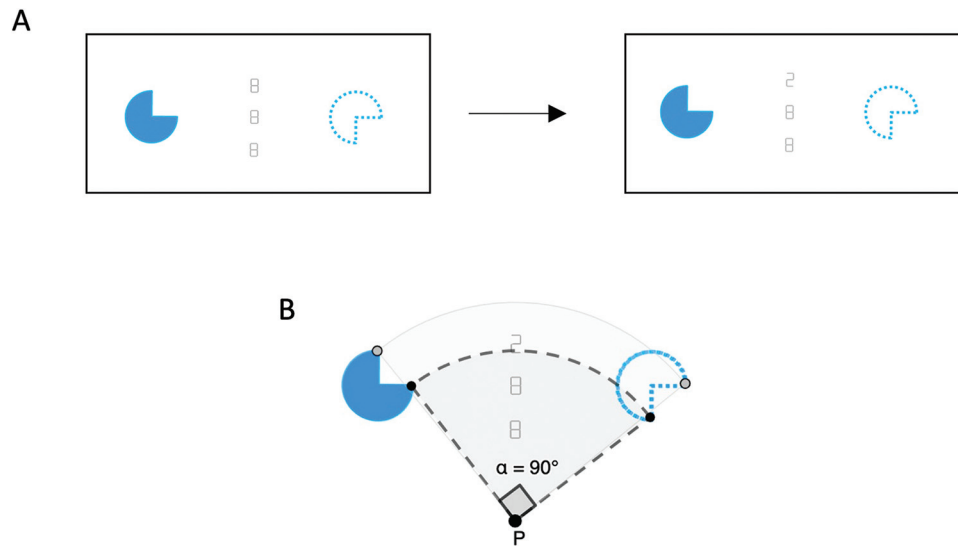
Stimuli and Procedure

The task was presented on a Dell OptiPlex 990 LCD monitor (19"; 1280 × 768 pixels; 60 Hz) at a viewing distance of ~ 50 cm. Stimuli were presented against a black background. Each trial began with a white fixation cross presented for 700 ms. Blue Pacmen-shaped objects (2°) then appeared on left and right sides of the placeholders (i.e., vertically positioned digits; Figure 1A). Pacmen alternated between left and right positions, oriented between 0° and 90° (upward) or 90° and 0° (downward). The ISI was 0 ms, as determined by a separate rating experiment (see OSF; see also Bermeitinger, 2013). After 25 frames (~ 450 ms), three gray placeholders, equally spaced in vertical alignment, appeared (.25° wide, .5° tall, each). After 200 ms, a target (☐ or ☐) was revealed at one of the three placeholders by removing two line-segments from the placeholders (☐; Figure 1A).

Participants were instructed to press a computer key ("F" for ☐ and "J" for ☐) as soon as they detected the target (i.e., "Respond as quickly, but as accurately, as possible."). The target remained onscreen until participants responded. Participants completed a

¹ Analyses, however, were subsequently based on a linear mixed-effects model, per recent recommendations. Sample size remains appropriate for these analyses.

Figure 1
An Illustration of the Stimuli and Task



Note. (A) A depiction of the trial prior to target presentation (left) and presentation of the target at the top placeholder (right). (B) An illustration of the curved trajectory according to kinematic geometry in the upward condition.² Point P is the unique center of rotation for the 90° angular difference (rotated by 90°) between the Pacmen. The gray solid line represents the kinematic path defined by Point P and the two gray points on the Pacmen. The black dashed line represents the kinematic path defined by Point P and the two black points on the Pacmen. See the online article for the color version of this figure.

total of 24 trials, with an equal number of upward and downward trials (random order).

Predictions

When two endpoints are clearly present, Newtonian physics minimizes the cost of energy involved in constructing the path of motion. In the present task, Newtonian physics describes a straight path (with concurrent rotation). Accordingly, in both conditions, apparent motion based on Newtonian physics overlapped with the middle position. By contrast, kinematic geometry minimizes the path itself, producing the shortest possible path of motion that most accurately preserves the invariant features of the object. In the present task, kinematic geometry describes a curved path based on the unique center of rotation given by the endpoints of position and angular difference of the objects. Accordingly, in the upward condition, apparent motion based on kinematics overlapped with the top position (Figure 1B), and in the downward condition, it overlapped with the bottom position. Thus, if apparent motion perception abides by Newtonian physics, then participants' responses should be slowest at the middle position, whereas if it abides by kinematic geometry, participants' responses should be slower when the targets overlap with the corresponding curved paths of motion.

Results

Analyses were conducted using R Version 3.5 and the lme4 R package (Bates et al., 2015). RT data were trimmed per participant and per condition based on the criterion of $M \pm 2 SD$. Three participants were excluded because of mean RTs exceeding 3000 ms. Only correct trials were analyzed. Error rate was 4.7%.

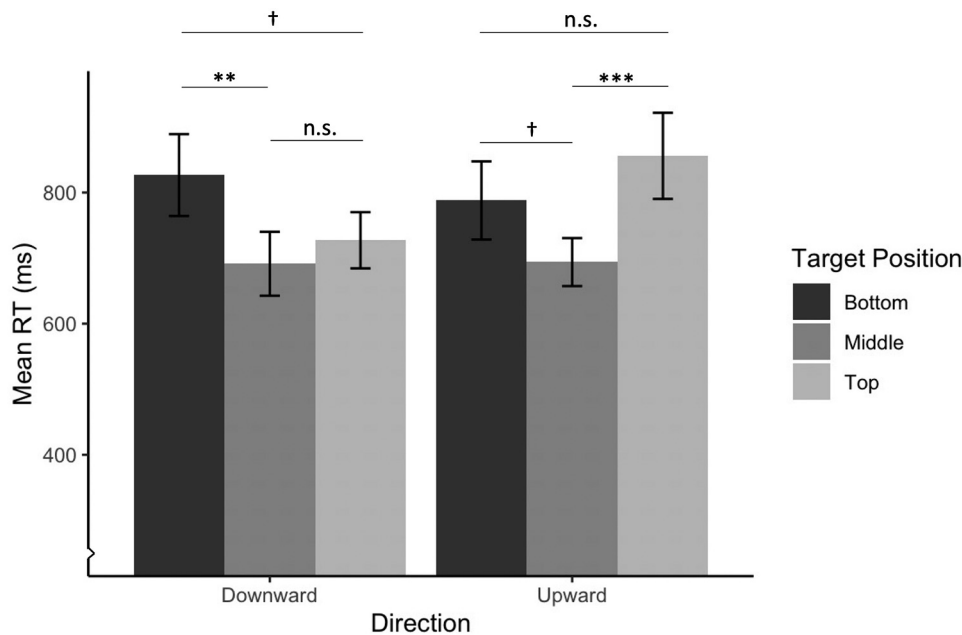
A linear mixed-effects analysis, with target position (top, middle, and bottom) and direction (upward or downward) as fixed factors, and random intercepts for participants as a random factor, revealed a significant main effect of target position, $F(2, 195) = 10.97, p < .001, \eta_p^2 = .10$, and a significant interaction between target position and direction, $F(2, 195) = 5.40, p = .005, \eta_p^2 = .05$ (see Figure 2). There was no main effect of direction ($p = .157, \eta_p^2 = .01$).

Given the significant interaction, post hoc comparisons based on estimated marginal means (Bonferroni corrected) were conducted separately for upward and downward trials. These analyses revealed that, in the downward trials, participants were significantly slower when the target appeared at the bottom position compared to the middle position, $M_{\text{difference}} = 135.3 \text{ ms}, t(195) = 3.60, p = .002, d = .52$. In the upward trials, participants were significantly slower at detecting the target when it appeared at the top position compared to the middle position, $M_{\text{difference}} = 162.0 \text{ ms}, t(195) = 4.32, p < .001, d = .62$. In both cases, the results are consistent with apparent motion perception along a curved path, as predicted by kinematic geometry, interfering with target detection.

However, an alternative possibility is that spatial position alone affected participants' responses, not the perception of apparent motion according to kinematic geometry. That is, perhaps participants were simply slower at detecting targets when they appeared at the extreme locations (i.e., top and bottom positions). Although the interaction between target position and direction would seem

² The curved path is based on the following equation: $r^2 = (x-h)^2 + (y-k)^2$; h and k represent the coordinates of the center of rotation P ; r is the radius (distance between the center of rotation and the object). The straight path is based on Maupertuis' principle of least action. See mathematical formulation in Carlton and Shepard (1990b).

Figure 2
Mean RTs for Both Downward and Upward Conditions



n.s.: non-significant ($p > .100$), † $p_{corrected} .050 - .100$, ** $p_{corrected} < .010$, *** $p_{corrected} < .001$

Note. Error bars represent 95% CI.

to rule out this possibility, we conducted additional comparisons to shed light on this issue. First, in the downward trials, target detection was marginally slower for the bottom position (curved path consistent with kinematics) compared to the top position (curved path not consistent with kinematics), $M_{\text{difference}} = 99.5$ ms, $t(195) = 2.65$, $p = .052$, $d = .38$. Although this effect did not reach statistical significance, it demonstrates that responses at the extreme locations were not uniformly slower. Second, and crucially, target detection during the downward trials was not significantly slower at the top position (curved path not consistent with kinematics) than the middle position (path consistent with Newtonian physics), $M_{\text{difference}} = 35.8$ ms, $t(195) = .96$, $p > .999$, $d = .14$, which is inconsistent with an explanation based exclusively on spatial position, at least during the downward trials.

What about the upward trials? Here, unlike the downward trials, there was not a significant difference between the extreme positions. In particular, target detection at the top position (curved path consistent with kinematics) was not significantly slower than at the bottom position (curved path not consistent with kinematics), $M_{\text{difference}} = 68.0$ ms, $t(195) = 1.81$, $p = .430$, $d = .26$. Moreover, in the upward trials, target detection was marginally slower at the extreme position that did not overlap with the kinematically specified curved path (bottom position) compared to the middle position, $M_{\text{difference}} = 94.0$ ms, $t(195) = 2.51$, $p = .078$, $d = .36$. Thus, the findings from the upward trials do not rule out an influence of spatial position. However, taken together with those from the downward trials, the

evidence suggests that apparent motion perception abides by kinematic geometry, although there may be some variation depending on the direction (upward vs. downward) of movement.

Discussion

The present study provides novel support for kinematic geometry as a computational constraint on apparent motion perception. We found that perception of a curved path, which was absent in the retinal input, but interpolated as a constructive process, interrupted target detection along this path, suggesting that apparent motion is dominated by kinematic geometry.

In a world where motion in the absence of external forces (such as friction, air resistance, and gravity) is not typical or representative, why would kinematic geometry dominate Newtonian physics in the perception of apparent motion? As noted in the introduction, the understanding of geometry appears to precede that of physics in development and, thus, may represent a more primary constraint on perception. Moreover, kinematic geometry represents the simpler motion, given that there are fewer parameters associated with the path of motion (i.e., translation over a circular path is encompassed within the path as opposed to potentially separate computations for translation and rotation).

A caveat to the present results is that they varied, to some extent, on the direction of movement (downward vs. upward). Why might this be? One possible explanation is that spatial position on this task did, to some extent, affect performance, although it is unknown why such an

effect would exist for the upward, but not downward, trials. Another possibility is that there are unaccounted effects related to Newtonian physics, particularly gravity, force, and momentum. Other research suggests that participants “undershoot” (compared to ground truth kinematics) on upward trials (McBeath & Shepard, 1989), perhaps because of initial forces. This is consistent with studies demonstrating that downward-moving stimuli result in larger forward displacement by participants than upward-moving stimuli (Hubbard, 2001; Nagai et al., 2002; see also Claassen et al., 2016; De Sá Teixeira et al., 2013). From this perspective, it would seem that principles of Newtonian physics may be incorporated along with kinematics, such that apparent motion perception is not based exclusively on kinematics (Prakash et al., 2020; Todorovič, 2001). Future research might consider addressing this possibility by manipulating the number and/or placement of placeholders in the task used here.

There is a well-known distinction between dorsal and ventral visual pathways (Goodale & Milner, 1992). Whereas the dorsal stream is known for its role in visually-guided action, the ventral stream is largely implicated in visual perception. Given the relevance of mass and forces when interacting with objects in the physical world, it is perhaps not surprising that the dorsal stream is relevant during tasks in which participants simulate action on objects (Hebart & Hesselmann, 2012). Consistent with this possibility is evidence that there is parietal activation when viewing dynamic physical scenes involving mass and forces (Fischer et al., 2016). The ventral stream, however, may play a greater role in tasks that involve processing geometric relations relevant for object perception, including motion-defined shapes, as in the present study (Kravitz et al., 2013). Nevertheless, because of the interactions between processing streams, it is possible that physical reasoning requiring Newtonian physics builds on kinematic geometry. Indeed, it is undoubtedly the case that an account of physical reasoning that combines kinematic geometry and Newtonian physics will prove most comprehensive.

References

- Anderson, S. F., Kelley, K., & Maxwell, S. E. (2017). Sample-size planning for more accurate statistical power: A method adjusting sample effect sizes for publication bias and uncertainty. *Psychological Science*, 28(11), 1547–1562. <https://doi.org/10.1177/0956797617723724>
- Bates, D., Maechler, N., Bolker, B., and Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Battaglia, P. W., Hamrick, J. B., & Tenenbaum, J. B. (2013). Simulation as an engine of physical scene understanding. *PNAS: Proceedings of the National Academy of Sciences of the United States of America*, 110(45), 18327–18332. <https://doi.org/10.1073/pnas.1306572110>
- Bermeitinger, C. (2013). Response priming with apparent motion primes. *Psychological Research*, 77(4), 371–387. <https://doi.org/10.1007/s00426-012-0436-x>
- Bramley, N. R., Gerstenberg, T., Tenenbaum, J. B., & Gureckis, T. M. (2018). Intuitive experimentation in the physical world. *Cognitive Psychology*, 105, 9–38. <https://doi.org/10.1016/j.cogpsych.2018.05.001>
- Buckley, C. L., Kim, C. S., McGregor, S., & Seth, A. K. (2017). The free energy principle for action and perception: A mathematical review. *Journal of Mathematical Psychology*, 81, 55–79. <https://doi.org/10.1016/j.jmp.2017.09.004>
- Carlton, E. H., & Shepard, R. N. (1990a). Psychologically simple motions as geodesic paths I. Asymmetric objects. *Journal of Mathematical Psychology*, 34(2), 127–188. [https://doi.org/10.1016/0022-2496\(90\)90001-P](https://doi.org/10.1016/0022-2496(90)90001-P)
- Carlton, E. H., & Shepard, R. N. (1990b). Psychologically simple motions as geodesic paths II. Symmetric objects. *Journal of Mathematical Psychology*, 34(2), 189–228. [https://doi.org/10.1016/0022-2496\(90\)90002-Q](https://doi.org/10.1016/0022-2496(90)90002-Q)
- Chater, N. (1996). Reconciling simplicity and likelihood principles in perceptual organization. *Psychological Review*, 103(3), 566–581. <https://doi.org/10.1037/0033-295X.103.3.566>
- Chong, E., Familiar, A. M., & Shim, W. M. (2016). Reconstructing representations of dynamic visual objects in early visual cortex. *PNAS: Proceedings of the National Academy of Sciences of the United States of America*, 113(5), 1453–1458. <https://doi.org/10.1073/pnas.1512144113>
- Claassen, J., Bardins, S., Spiegel, R., Strupp, M., & Kalla, R. (2016). Gravity matters: Motion perceptions modified by direction and body position. *Brain and Cognition*, 106, 72–77. <https://doi.org/10.1016/j.bandc.2016.05.003>
- Dayan, E., Casile, A., Levit-Binnun, N., Giese, M. A., Hendl, T., & Flash, T. (2007). Neural representations of kinematic laws of motion: Evidence for action-perception coupling. *PNAS: Proceedings of the National Academy of Sciences of the United States of America*, 104(51), 20582–20587. <https://doi.org/10.1073/pnas.0710033104>
- Deeb, A.-R., Cesanek, E., & Domini, F. (2021). Newtonian predictions are integrated with sensory information in 3D motion perception. *Psychological Science*, 32(2), 280–291. <https://doi.org/10.1177/0956797620966785>
- De Sá Teixeira, N. A., Hecht, H., & Oliveira, A. M. (2013). The representational dynamics of remembered projectile locations. *Journal of Experimental Psychology: Human Perception and Performance*, 39(6), 1690–1699. <https://doi.org/10.1037/a0031777>
- Fischer, J., Mikhael, J. G., Tenenbaum, J. B., & Kanwisher, N. (2016). Functional neuroanatomy of intuitive physical inference. *Proceedings of the National Academy of Sciences of the United States of America*, 113(34), E5072–E5081. <https://doi.org/10.1073/pnas.1610344113>
- Foster, D. H. (1978). *Visual apparent motion and the calculus of variations*. Wiley.
- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 15(1), 20–25. [https://doi.org/10.1016/0166-2236\(92\)90344-8](https://doi.org/10.1016/0166-2236(92)90344-8)
- Hanc, J., & Taylor, E. F. (2004). From conservation of energy to the principle of least action: A story line. *American Journal of Physics*, 72(4), 514–521. <https://doi.org/10.1119/1.1645282>
- Hamrick, J. B., Battaglia, P. W., Griffiths, T. L., & Tenenbaum, J. B. (2016). Inferring mass in complex scenes by mental simulation. *Cognition*, 157, 61–76. <https://doi.org/10.1016/j.cognition.2016.08.012>
- Hebart, M. N., & Hesselmann, G. (2012). What visual information is processed in the human dorsal stream? *The Journal of Neuroscience*, 32(24), 8107–8109. <https://doi.org/10.1523/JNEUROSCI.1462-12.2012>
- Hecht, H., & Bertamini, M. (2000). Understanding projectile acceleration. *Journal of Experimental Psychology: Human Perception and Performance*, 26(2), 730–746. <https://doi.org/10.1037/0096-1523.26.2.730>
- Hecht, H., & Proffitt, D. R. (1991). Apparent extended body motions in depth. *Journal of Experimental Psychology: Human Perception and Performance*, 17(4), 1090–1103. <https://doi.org/10.1037/0096-1523.17.4.1090>
- Hidaka, S., Nagai, M., Sekuler, A. B., Bennett, P. J., & Gyoba, J. (2011). Inhibition of target detection in apparent motion trajectory. *Journal of Vision*, 11(10), Article 2. <https://doi.org/10.1167/11.10.2>
- Hubbard, T. L. (2001). The effect of height in the picture plane on the forward displacement of ascending and descending targets. *Canadian Journal of Experimental Psychology*, 55(4), 325–329. <https://doi.org/10.1037/h0087380>
- Kim, I.-K., & Spelke, E. S. (1999). Perception and understanding of effects of gravity and inertia on object motion. *Developmental Science*, 2(3), 339–362. <https://doi.org/10.1111/1467-7687.00080>
- Kravitz, D. J., Saleem, K. S., Baker, C. I., Ungerleider, L. G., & Mishkin, M. (2013). The ventral visual pathway: An expanded neural framework

- for the processing of object quality. *Trends in Cognitive Sciences*, 17(1), 26–49. <https://doi.org/10.1016/j.tics.2012.10.011>
- Lourenco, S. F., & Huttenlocher, J. (2008). The representation of geometric cues in infancy. *Infancy*, 13(2), 103–127. <https://doi.org/10.1080/15250000701795572>
- Mach, E. (1914). *The analysis of sensations and the relation of the physical to the psychical* (3rd rev. ed). Open Court. <https://doi.org/10.2307/3604840>
- McBeath, M. K., & Shepard, R. N. (1989). Apparent motion between shapes differing in location and orientation: A window technique for estimating path curvature. *Perception & Psychophysics*, 46(4), 333–337. <https://doi.org/10.3758/BF03204986>
- Mousavi, S., & Sunder, S. (2019). *Physical laws and human behavior: A three-tier framework*. Cowles Foundation for Research in Economics.
- Muckli, L., Kohler, A., Kriegeskorte, N., & Singer, W. (2005). Primary visual cortex activity along the apparent-motion trace reflects illusory perception. *PLoS Biology*, 3(8), Article e265. <https://doi.org/10.1371/journal.pbio.0030265>
- Nagai, M., Kazai, K., & Yagi, A. (2002). Larger forward memory displacement in the direction of gravity. *Visual Cognition*, 9(1–2), 28–40. <https://doi.org/10.1080/13506280143000304>
- Prakash, C., Stephens, K. D., Hoffman, D. D., Singh, M., & Fields, C. (2020). Fitness beats truth in the evolution of perception. *Acta Biotheoretica*. Advance online publication. <https://doi.org/10.1007/s10441-020-09400-0>
- Restle, F. (1979). Coding theory of the perception of motion configurations. *Psychological Review*, 86(1), 1–24. <https://doi.org/10.1037/0033-295X.86.1.1>
- Sanders, L. L. O., Aukstulewicz, R., Hohlefeld, F. U., Busch, N. A., & Sterzer, P. (2014). The influence of spontaneous brain oscillations on apparent motion perception. *NeuroImage*, 102, 241–248. <https://doi.org/10.1016/j.neuroimage.2014.07.065>
- Schwartz, M., & Day, R. H. (1979). Visual shape perception in early infancy. *Monographs of the Society for Research in Child Development*, 44(7), 1–63. <https://doi.org/10.2307/1165963>
- Searle, J. A., & Hamm, J. P. (2017). Mental rotation: An examination of assumptions. *Wiley Interdisciplinary Reviews: Cognitive Science*, 8(6), Article e1443. <https://doi.org/10.1002/wcs.1443>
- Shen, L., Han, B., & de Lange, F. P. (2020). Apparent motion induces activity suppression in early visual cortex and impairs visual detection. *The Journal of Neuroscience*, 40(28), 5471–5479. <https://doi.org/10.1523/JNEUROSCI.0563-20.2020>
- Shepard, R. N. (1994). Perceptual–cognitive universals as reflections of the world. *Psychonomic Bulletin & Review*, 1(1), 2–28. <https://doi.org/10.3758/BF03200759>
- Shepard, R. N. (2001). Perceptual-cognitive universals as reflections of the world. *Behavioral and Brain Sciences*, 24(4), 581–601.
- Shepard, R. N., & Judd, S. A. (1976). Perceptual illusion of rotation of three-dimensional objects. *Science*, 191(4230), 952–954. <https://doi.org/10.1126/science.1251207>
- Slater, A., & Morison, V. (1985). Shape constancy and slant perception at birth. *Perception*, 14(3), 337–344. <https://doi.org/10.1068/p140337>
- Spelke, E. S., Katz, G., Purcell, S. E., Ehrlich, S. M., & Brehm, K. (1994). Early knowledge of object motion: Continuity and inertia. *Cognition*, 51(2), 131–176. [https://doi.org/10.1016/0010-0277\(94\)90013-2](https://doi.org/10.1016/0010-0277(94)90013-2)
- Todorović, D. (2001). Is kinematic geometry an internalized regularity? *Behavioral and Brain Sciences*, 24(4), 641–651. <https://doi.org/10.1017/S0140525X01000073>
- Tse, P. U. (2006). Neural correlates of transformational apparent motion. *NeuroImage*, 31(2), 766–773. <https://doi.org/10.1016/j.neuroimage.2005.12.029>
- Wagemans, J., Feldman, J., Gepshtein, S., Kimchi, R., Pomerantz, J. R., van der Helm, P. A., & van Leeuwen, C. (2012). A century of Gestalt psychology in visual perception: II. Conceptual and theoretical foundations. *Psychological Bulletin*, 138(6), 1218–1252. <https://doi.org/10.1037/a0029334>
- Werkhoven, P., Snippe, H. P., & Koenderink, J. J. (1990). Effects of element orientation on apparent motion perception. *Perception & Psychophysics*, 47(6), 509–525. <https://doi.org/10.3758/BF03203104>
- Yantis, S., & Nakama, T. (1998). Visual interactions in the path of apparent motion. *Nature Neuroscience*, 1(6), 508–512. <https://doi.org/10.1038/2226>

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