

Enhanced discriminability for nonbiological motion violating the two-thirds power law

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The two-thirds power law describes the relationship between velocity and curvature in human motor movements. Interestingly, this motor law also affects visual motion perception, in which stimuli moving according to the two-thirds power law are perceived to have a constant velocity compared to stimuli actually moving at constant velocity. Thus, visual motion

adhering to biological motion principles causes a kinematic illusion of smooth and velocity-invariant motion. However, it is yet unclear how this motion law affects the discrimination of visual stimuli and if its encoding requires attention. Here we tested the perceptual discrimination of stimuli following biological (two-thirds power law) or nonbiological movement

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under conditions in which the stimuli were degraded or masked through continuous flash suppression. Additionally, we tested subjective perception of naturalness and velocity consistency. Our results show that the discriminability of a visual target is inversely related to the perceived “naturalness” of its movement. Discrimination of stimuli following the two-thirds power law required more time than the same stimuli moving at constant velocity or nonecological variants of the two-thirds power law and was present for both masked and degraded stimuli.

Introduction

Humans are highly sensitive to the perception of biological motion (Blake & Shiffrar, 2007, but see Hiris, 2007). Since the early experiments of Johansson (1973), many studies have shown that the visual system is specifically tuned to detect biological motion, enabling the recognition of animacy early in development (Bertenthal & Fischer, 1978; Bertenthal, Proffitt, & Cutting, 1984; Fox & McDaniel, 1982; Simion, Regolin, & Bulf, 2008) as well as conveying a wealth of information regarding the actions (Dittrich, 1993), gender (Mather & Murdoch, 1994; Pollick, Lestou, Ryu, & Cho, 2002), and identity (Loula, Prasad, Harber, & Shiffrar, 2005; Troje, Westhoff, & Lavrov, 2005) of point-light display walkers. A fundamental law of human motor kinematics is the two-thirds power law, which describes the relationship between velocity and curvature in biological motion (Abend, Bizzi, & Morasso, 1982; Lacquaniti, Terzuolo, & Viviani, 1983; Viviani & Flash, 1995; Viviani & Terzuolo, 1982). This law states that the velocity of the effector increases along the part where the curvature is small and decreases along the parts where the curvature is large. Considering an angular (A) or tangential (V) velocity, the law can be expressed as $A(t) = K \times C(t)^{2/3}$ or $V(t) = K \times R(t)^{1/3}$ where R is the curvature radius, $C(t) = 1/R(t)$ is the curvature of the trajectory, and K is the velocity gain factor. The two-thirds power law describes human biological motion for two-dimensional and three-dimensional arm movements (Soechting, Lacquaniti, & Terzuolo, 1986), passive hand movements (Viviani, Baud-Bovy, & Redolfi, 1997), eye movements (de'Sperati & Viviani, 1997), speech production (Perrier & Fuchs, 2008; Tasko & Westbury, 2004), and locomotion (Pham, Hicheur, Arechavaleta, Laumond, & Berthoz, 2007; Vieilledent, Kerlirzin, Dalbera, & Berthoz, 2001).

Interestingly, it has been found that the two-thirds power law also affects perceptual judgments in the absence of motor action, impacting motion imagery (Papaxanthis, Paizis, White, Pozzo, & Stucchi, 2012),

motion prediction (Kandel, Orliaguet, & Viviani, 2000), and velocity perception (Levit-Binnun, Schechtman, & Flash, 2006; Viviani et al., 1997; Viviani & Stucchi, 1992). For example, it has been shown that visual motion following the two-thirds power law, despite having a variable velocity, is perceived as having a constant velocity (Viviani & Stucchi, 1992). This has been interpreted as evidence that motor representations influence visual motion perception (Casile & Giese, 2006; Dayan et al., 2007; Hommel, Musseler, Aschersleben, & Prinz, 2001). Indeed, training on motor actions violating the two-thirds power law results in improvements in perception of visual motion violating this law (Beets, Rösler, & Fiehler, 2010). Finally, viewing biological motion following the two-thirds power law is associated with activation of specific neural structures, such as frontal medial and premotor regions (Casile et al., 2010; Dayan et al., 2007), showing that the human brain is selectively sensitive to this kinematic law.

Thus, these results suggest that the human visual system has a constitutive perceptual bias based on kinematic laws of biological motion. Specifically, this bias leads to a perceptual illusion in which movement adhering to the two-thirds power law is perceived as constant compared to actual Euclidean constant velocity. However, it is not clear if this subjective illusion would also affect objective measures of perception. One possibility is that the subjective stabilization of velocity enabled by the two-thirds power law motion allows faster discrimination of visual targets moving in accordance with this biological motion profile. Alternatively, it is possible that a motion violating the two-thirds power law is perceived as less natural and thus attracts more attention, resulting in faster visual discrimination. Furthermore, although humans show a high sensitivity to perception of biological motion (Ahlström, Blake, & Ahlström, 1997; Johansson, 1973), which develops early in infancy and is thought to rely on low-level mechanisms (Mather, Radford, & West, 1992; Simion et al., 2008), it is yet under debate if biological motion perception is preattentive or postattentive (Thompson & Parasuraman, 2012; Thornton, Rensink, & Shiffrar, 2002; Thornton & Vuong, 2004). Previous work has shown that dynamic facial expressions (Faivre, Charron, Roux, Lehericy, & Kouider, 2012), translational and rotational motion (Kaunitz, Fracasso, Lingnau, & Melcher, 2013), or biological motion (Faivre & Koch, 2014) can be processed unconsciously and thus arguably without explicit attention. This suggests that some processes relating to perception of biological motion may not require attention; however, this has not been investigated for fundamental kinematic laws such as the

two-thirds power law, which would allow addressing this issue without the additional complexities of human figural processing as in point-light displays. In this study, we first aimed at investigating whether the discrimination of visual motion targets varies based on their agreement with biological movement parameters (i.e., the two-thirds power law) and if this is related to the subjective feeling of motion naturalness and smoothness. We then measured target discriminability by motion type objectively by measuring the time necessary to discriminate the orientation of a simple visual stimulus moving according to the two-thirds power law or violating it. Finally, we investigated whether the processing of kinematic laws relied on explicit attention by comparing biological motion masked through continuous flash suppression (CFS) with nonmasked biological motion. To this end, we employed the breaking CFS (bCFS) paradigm, which is an established measure of invisible stimulus processing (Maruya, Yang, & Blake, 2007; Salomon, Kaliuzhna, Herbelin, & Blanke, 2015; Tsuchiya & Koch, 2005). bCFS relies on the simultaneous presentation of separate images to the two eyes. The dominant eye is presented with high-contrast images, which suppress the target image presented to the other eye. The measured variable is the time necessary for the subject to break interocular suppression and thus consciously perceive the target stimulus. We hypothesized that nonbiological motion would be subjectively perceived as less natural than biological motion following the two-thirds power law, causing it to be discriminated faster. Following previous findings showing the involvement of both high- and low-level mechanisms in biological motion perception (Thornton et al., 2002; Thornton & Vuong, 2004) a decreased discriminability of nonbiological motion stimuli for both masked and unmasked displays was considered equally likely.

Methods

Participants were 55 right-handed healthy volunteers (18 females) from the student population at Ecole Polytechnique Fédérale de Lausanne (EPFL). Their ages ranged from 18 to 30 years ($M = 22.7$ years, $SD = 3.0$ years). All participants had normal or corrected-to-normal sight and no psychiatric or neurological history. They participated in the study for payment (20 Swiss francs). All participants were naive to the purpose of the study and gave informed consent, and the study was approved by the ethics committee of EPFL. Each experiment was conducted with different participants.

Experiment 1

Participants

Nineteen participants (three females) participated in Experiment 1. Their ages ranged from 18 to 30 years ($M = 23.6$ years, $SD = 3.2$ years).

Visual stimuli

Stimuli consisted of high-contrast dynamic noise patch suppressors (“Mondrians”; Salomon, Lim, Herbelin, Hesselmann, & Blanke, 2013) and target stimuli. The target stimuli consisted of a solid black (RGB 0, 0, 0) line (1.5° of visual angle) tilted either 45° to the left or to the right on a gray (RGB 229, 229, 229) background.

Stimuli motion

The target stimuli moved along an elliptic path centered on a black fixation cross (3.5° of visual angle) in the middle of the screen (Figure 1). The major semiaxis of the ellipse was 11.7° of visual angle, and the minor semiaxis was 5.8° of visual angle. The line was tilted clockwise in half the trials and counterclockwise in the other half. There were two types of motion based on 172 couples (x, y) of coordinates. These coordinates were updated at each frame on the screen (every 16 ms). Two different motions were used; in one, a constant velocity was maintained along the full axis of the ellipse, and the other followed the two-thirds power law velocity. The starting point of the movement along the ellipse was defined randomly in each trial (see Supplementary Movie 1 for demonstration of stimuli and motion profiles).

Stimuli were presented using ExpyVR, custom-built multimedia stimuli presentation software developed with Python 2.6 and the Open Graphics Library v.2.2 (available at <http://lnc0.epfl.ch/>). The stimuli were viewed via a head-mounted display (HMD; Oculus VR, 110° diagonal field of view, refresh rate 60 Hz).

Procedures

At the beginning of the experiment, participants filled in a questionnaire for demographic data. They were then tested for ocular dominance using the Dolman method, also known as the hole-in-the-card test (Cheng, Yen, Lin, Hsia, & Hsu, 2004). Participants were then fitted with the HMD, which allowed them to view only the experimental display and not their surroundings.

The experiment contained two parts: a subjective rating part (40 trials) and a detection part (256 trials per subpart). The total duration of the experiment was about 1 hr.

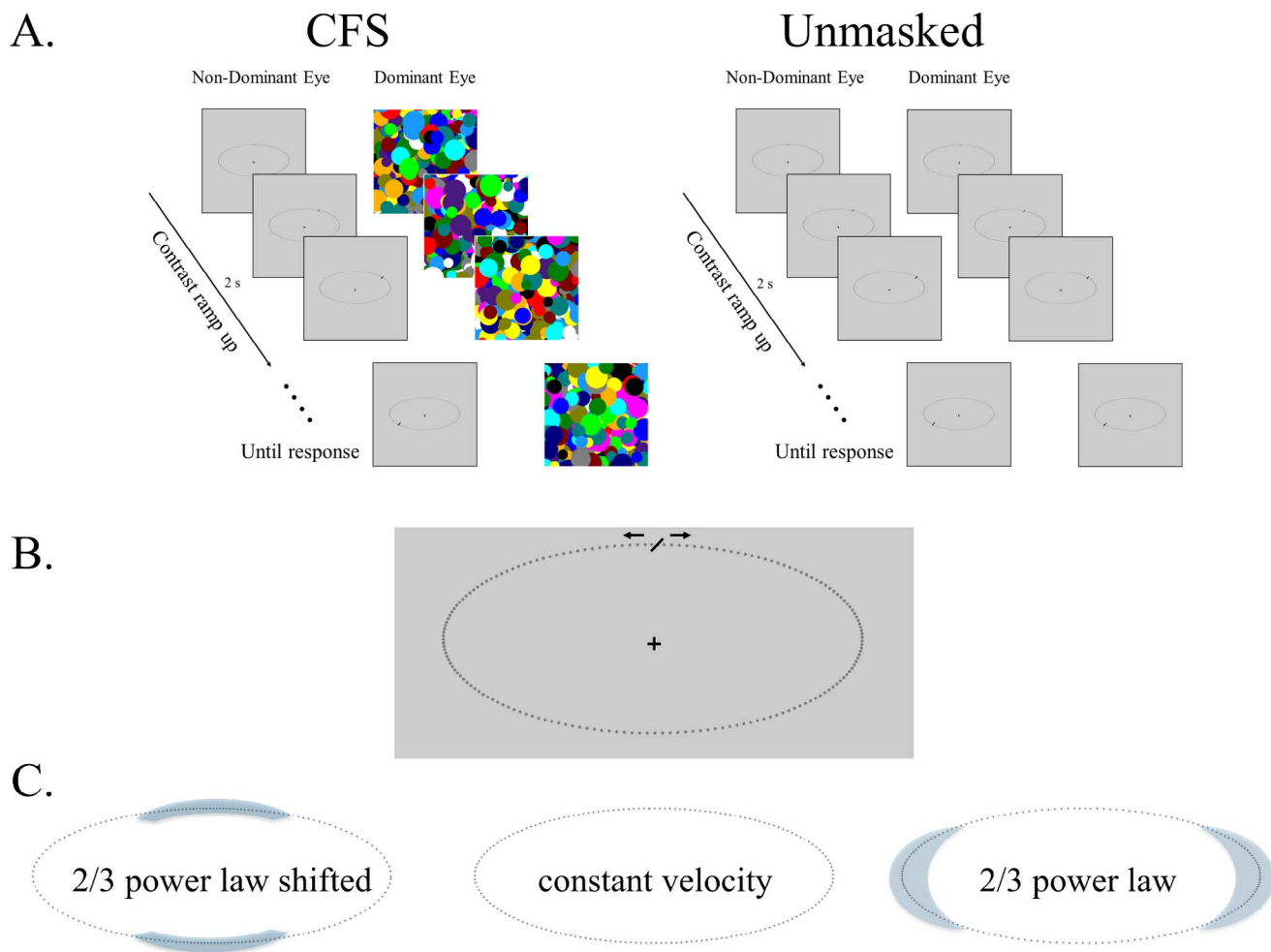


Figure 1. Experimental design. (A) CFS (left) and unmasked (right) paradigms. (B) Example of target stimulus (angled line), which was moving either clockwise or counterclockwise. Stimulus first appeared in a random location. Target contrast was ramped up over 2 s to avoid breaking CFS due to abrupt onset. Note dotted ellipse and arrows are for demonstration purposes only and were not visible to participants. (C) Scatterplots of stimulus motion at constant sampling rate. Density of dots represents the velocity of the movement; regions of higher density representing lower velocity are marked with blue outline. Ellipse and color are for demonstration purposes and were not present in the display.

Subjective ratings: Following Viviani and Stucchi (1992), we measured subjective perceptual judgments related to the perceived velocity and added a novel measurement regarding the perceived “naturalness” of the stimuli. Participants were shown the tilted line moving for 5 s to in both eyes and then asked two questions: “How did you perceive the velocity of the dot? Constant/Variable” and “How natural was the motion? 1 = Very natural to 6 = Very strange.”

Detection task: Participants were instructed to indicate as quickly as possible the orientation of the line. Their reaction time and accuracy were measured. There were two subparts. The first one was the CFS condition in which Mondrians were rapidly (10 Hz) flashed to the participants’ dominant eye and the target stimulus was presented simultaneously to the other eye. As in previous

bCFS experiments, the contrast of the target line was linearly ramped up from zero to reach a maximal value 2 s after its onset to avoid breaking CFS due to an abrupt onset (e.g., Mudrik, Breska, Lamy, & Deouell, 2011; Salomon, Galli, et al., 2015; Salomon, Kaliuzhna, et al., 2015). The trial ended when participants pressed the left or right arrow key on the keyboard to indicate their response. Target tilt and motion direction were randomized between trials. The second part was the conscious condition. It was exactly the same as the CFS condition; participants were presented with the target stimulus, with a 2-s contrast ramp as in the CFS condition except that here it was shown to both eyes and no Mondrian masks were presented. This condition with no flash suppression was designed to test for effects stemming from postperceptual processes. It allows one to control for possible differences

in detection time due to response or detection criteria. As is typically done in such CFS studies, the control condition always followed the non-CFS condition to avoid extensive exposure to the stimuli (e.g., Salomon, Lim, Herbelin, et al., 2013; Salomon, Kaliuzhna, et al., 2015).

Experiment 2

Experiment 2 was designed to investigate if the difference between the two motions in Experiment 1 were due to the variance in the velocity between the two motions or to the velocity profile itself.

Participants

Eighteen participants (five females) participated in Experiment 2. Their ages ranged from 18 to 29 years ($M = 22.7$ years, $SD = 3.3$ years).

Visual stimuli and procedures

The stimuli and procedures were the same as in Experiment 1 except for the types of motion that were used. In this experiment, the two motions compared were the constant velocity and the shifted two-thirds power law velocity. This shifted two-thirds power law was created by applying a 90° shift to the velocity profile corresponding to the two-thirds power law. This motion had the exact same velocity variance as the regular two-thirds power law, but the acceleration was this time in the curved part and the deceleration in the straight part of the ellipse. Thus, in this experiment, each motion profile violated the two-thirds power law in a distinct way.

Experiment 3

Experiment 3 was designed to compare the two-thirds power law velocity to the shifted two-thirds power law velocity.

Participants

Eighteen participants (10 females) participated in Experiment 3. Their ages ranged from 19 to 25 years ($M = 21.9$ years, $SD = 1.8$ years).

Visual stimuli and procedures

The stimuli and procedures were the same as in Experiment 1 except for the two motions compared, which were the two-thirds power law velocity and the shifted two-thirds power law velocity.

Data analysis

The data were analyzed with JASP (Love et al., 2015) and Matlab R 2013b (The Mathworks, Natick, MA). Erroneous trials or trials with reaction times (RTs) deviating more than three times from the participant's mean were discarded (less than 1% of trials). The differences in subjective judgments were tested with the Kolmogorov-Smirnov and Wilcoxon rank sum tests. Accuracy and RTs were tested using a 2×2 repeated-measures ANOVA with visibility (CFS/unmasked) and movement type (biological/nonbiological) as factors. For visualization purposes, naturalness ratings were inverted in the figures such that a higher rating implied a higher feeling of naturalness.

Results and discussion

Experiment 1

Subjective judgments

Participants rated more frequently the two-thirds power law motion profile as following a constant velocity ($M = 75.0\%$ of the time, $SD = 15.1\%$) than the actual constant velocity motion ($M = 22.2\%$ of the time, $SD = 22.9\%$, $KS = 0.77$, $p = 0.00001$). They also rated the two-thirds power law motion as more natural than the constant motion ($M = 2.25$, $SD = 1.16$ vs. $M = 3$, $SD = 1.02$; $Z = -3.68$, $p = 0.0002$). Thus, in line with previous findings (Lupyan & Ward, 2013), the two-thirds power law motion was perceived as having a more constant velocity than true constant velocity movement. Furthermore, this motion was perceived as more natural to the observers (Figure 2).

RTs

The repeated-measures ANOVA indicated a significant effect of motion type on RTs, $F(1, 18) = 5.4$, $p = 0.03$, $\eta^2 = 0.23$, with longer RTs for two-thirds power law motion ($M = 4.29$, $SD = 0.18$) than constant motion ($M = 4.23$, $SD = 0.18$). As expected, we found longer RTs in the CFS condition ($M = 5.03$, $SD = 1$) versus the unmasked condition ($M = 3.5$, $SD = 0.6$), $F(1, 18) = 99$, $p = 0.00000001$, $\eta^2 = 0.84$. No interaction was found between the factors ($p = 0.25$).

Accuracy

The target was correctly discriminated in 97.2% ($SD = 2.0\%$) of trials in the CFS condition and 97.7% ($SD = 1.6\%$) in the conscious condition. The repeated-measures ANOVA indicated no effects of visibility or movement type on the accuracy rates (all $ps > 0.14$).

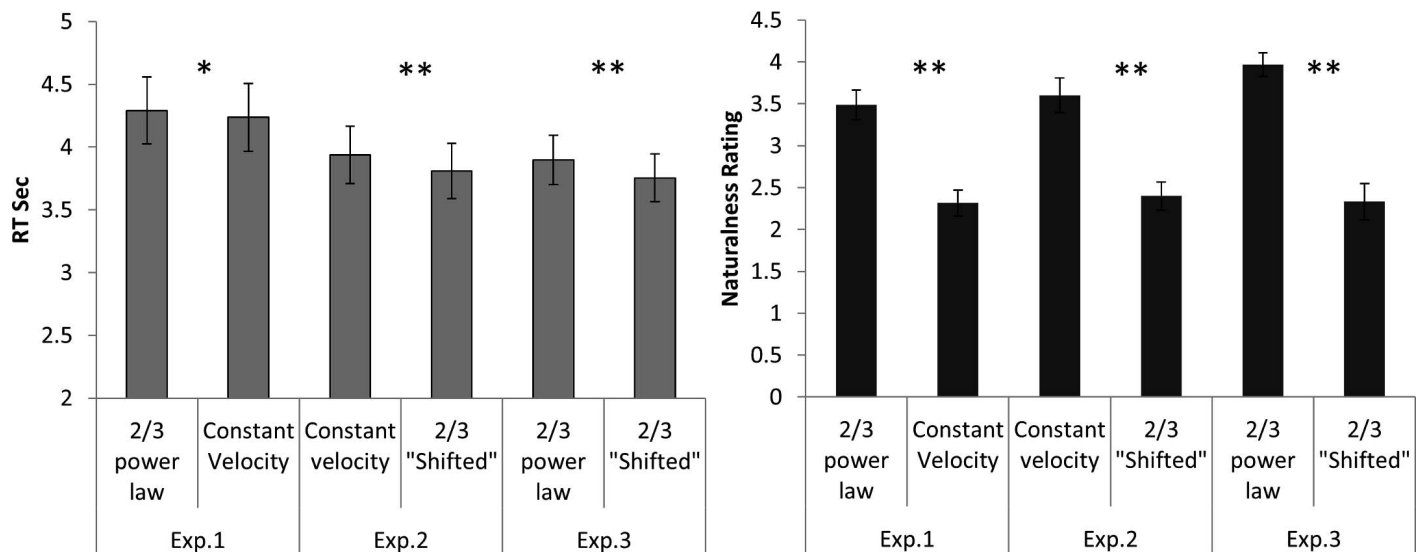


Figure 2. RTs and naturalness ratings for all experiments. RTs (left) and naturalness ratings (right) by movement type for all experiments. Note movement types violating the two-thirds power law were consistently rated to be less natural and were discriminated more rapidly in all three experiments. Error bars denote *SEM*.

Discussion

The results obtained in Experiment 1 show that motion following the two-thirds power law was perceived as more constant than motion with an actual constant velocity. Furthermore, RTs corresponding to motion following the two-thirds power law were longer, suggesting better visual discrimination for targets moving at constant motion velocity. However, it could be that these effects stemmed from a difference in the velocity profile's variance rather than from the biological motion law itself as the constant velocity presents much less variance than the two-thirds power law, which presents strong accelerations and decelerations. In Experiment 2, we tested whether this result was related to the velocity profile itself (i.e., the location of the velocity variance) by comparing the constant velocity with a shifted version of the two-thirds power law, which shared the same velocity variance as in the two-thirds power law but in which the velocity changes occurred on the noncurved section of the motion, thus violating the biological aspect of the two-thirds power law.

Experiment 2

Subjective judgments

Participants rated the velocity of the shifted two-thirds power law as being less constant ($M = 5.8\%$ of trials, $SD = 8.7\%$) than the constant velocity ($M = 53.9\%$ of trials, $SD = 21.7\%$, $KS = 0.83$, $p = 0.000001$). The ratings of naturalness for the shifted two-thirds power law ($M = 2.1$, $SD = 0.7$) were lower ($Z = 3.6$, $p =$

0.0003) than the ratings for the constant motion ($M = 3.6$, $SD = 0.8$). The ratings for the shifted two-thirds power law were thus opposite to the two-thirds power law compared to the constant velocity. Given that both the two-thirds power law and the shifted two-thirds power law have exactly the same velocity variance, this indicates that ratings were not related to the velocity variance per se, but rather to the location of the velocity changes on the ellipse.

RTs

The repeated-measures ANOVA indicated a significant effect of motion type on RTs, $F(1, 17) = 29.4$, $p = 0.00005$, $\eta^2 = 0.63$, with longer RTs for constant motion ($M = 3.93$, $SD = 0.95$) than the shifted two-thirds power law ($M = 3.80$, $SD = 0.91$). As expected, a difference in RTs between the CFS condition ($M = 4.59$, $SD = 0.24$) and the unmasked condition ($M = 3.1$, $SD = 0.14$) was found, $F(1, 17) = 79.3$, $p = 0.000001$, $\eta^2 = 0.84$. No interaction was found between the factors ($p = 0.44$).

Accuracy

The target was correctly discriminated in 96.3% ($SD = 2.0\%$) of trials in the CFS condition and 95.6% ($SD = 4.1\%$) in the conscious condition. The effect of movement type neared significance, $F(1, 17) = 3.91$, $p = 0.064$, with higher accuracy in the two-thirds shifted motion profile ($M = 96\%$, $SD = 3.3\%$) than in the constant motion profile ($M = 95.5\%$, $SD = 4.1\%$). The repeated-measures ANOVA indicated no effect of

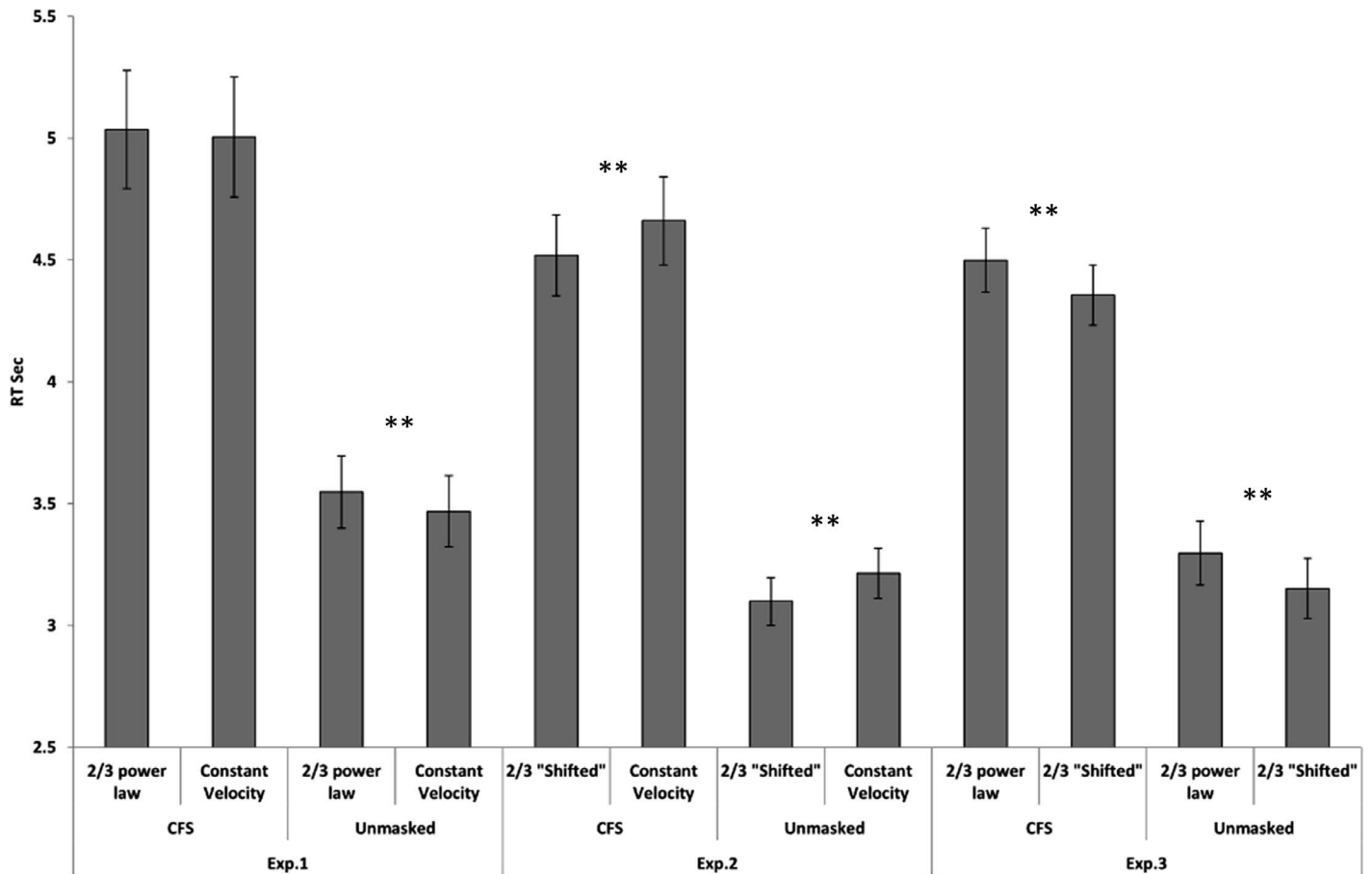


Figure 3. RTs for all experimental conditions. RTs by movement type and visibility type for all experiments. Note, ** denote $p < 0.01$. Error bars denote SEM.

visibility nor any interaction between motion type and visibility on the accuracy rates (all p s > 0.2).

Discussion

Experiment 2 indicated that the difference in the velocity variance between the two-thirds and constant motion could not explain the longer RTs for the two-thirds power law targets as when the same velocity variance was shifted spatially an opposite result was found with faster RTs for the shifted two-thirds power law targets. However, the shifted two-thirds power law stimuli were perceived as less natural and were discriminated more rapidly than the constant motion targets. Interestingly, both the perceived velocity variance and subjective ratings of naturalness for the constant velocity motion profile varied considerably between Experiments 1 and 2. This suggests that participants generated their judgments of velocity variability and naturalness by comparing the two stimuli they viewed. Thus, when the constant motion profile was paired with the two-thirds power law, it was viewed as having a variable motion and being less

natural, but when it was compared with the shifted two-thirds power law profile, it was perceived as more constant and natural. In Experiment 3, we therefore tested two motion profiles that were identical in terms of the velocity variance but differed in their spatial configuration, comparing biological motion in accordance with the two-thirds power law and the shifted two-thirds power law, which is the same motion profile but spatially shifted.

Experiment 3

Subjective judgments

Participants rated the two-thirds power law as being more constant ($M = 69.4\%$ of the time, $SD = 20.3\%$) than the shifted two-thirds power law ($M = 6.7\%$ of the time, $SD = 11.1\%$, $KS = 0.88$, $p = 0.000002$). The shifted two-thirds power law was also perceived as less natural ($Z = -4.41$, $p = 0.00001$) to the participants ($M = 3.7$, $SD = 0.9$) than the two-thirds power law velocity ($M = 2.0$, $SD = 0.6$).

RTs

The repeated-measures ANOVA indicated a significant effect of motion type on RTs, $F(1, 17) = 48$, $p = 0.000002$, $\eta^2 = 0.73$, with longer RTs for two-thirds power law motion ($M = 3.89$, $SD = 0.81$) than the shifted two-thirds power law ($M = 3.75$, $SD = 0.78$). As expected, a difference in RTs was found between the CFS condition in which they were longer ($M = 4.41$, $SD = 0.5$) than in the unmasked condition ($M = 3.2$, $SD = 0.5$), $F(1, 17) = 71.7$, $p = 0.000001$, $\eta^2 = 0.8$. No interaction was found between the factors ($p = 0.95$). See Figure 3 and Table 1 for full details of RTs.

Accuracy

The target was correctly discriminated in 95.1% ($SD = 4.0\%$) of trials in the CFS condition and 94.5% ($SD = 4.7\%$) in the unmasked condition. The repeated-measures ANOVA indicated neither effects of visibility or movement type nor any interaction on the accuracy rates (all $ps > 0.2$).

Discussion

Experiment 3 indicated that, for a given velocity variance, when the motion follows the two-thirds power law it is perceived as more constant in its velocity and more natural. Extending the results obtained in Experiments 1 and 2, we found that targets moving in accordance with the two-thirds power law were discriminated less rapidly.

General discussion

Several findings arise from these experiments: First, at the subjective level, targets moving according to the two-thirds power law were perceived as more natural and as having a more constant velocity than targets moving at a constant speed or following the shifted two-thirds power law. Second, RTs to stimuli moving according to the two-thirds power law were longer compared to stimuli moving with a nonbiological motion profile. This effect was present for both visible stimuli and stimuli masked by CFS. This finding suggests that targets following nonbiological motion are discriminated more rapidly compared to those following biological motion, at least when using a simple nonbodily form. This is, to the best of our knowledge, the first report of enhanced processing for nonbiological movement stimuli.

At the subjective level, our results replicate previous findings showing that visual motion following the two-thirds power law is perceived as moving

constantly despite having a variable velocity (Levit-Binnun et al., 2006; Viviani et al., 1997; Viviani & Stucchi, 1992). Extending these results, we show that motion following the two-thirds power law also appears to be more natural (Experiments 1 and 3)—this effect not being due to the velocity variance but rather to the spatiotemporal profile specific to the two-thirds power law (Experiment 2). This suggests that the kinematics of biological motion are perceived as familiar and natural even when presented in a nonbodily context. Interestingly, participants gave clear and consistent ratings of naturalness for the motion of a simple stimuli despite having no instruction on how to make this inference, suggesting an intuitive perception of the naturalness of biological motion. Furthermore, our data show a “hierarchy” of naturalness in which motion kinematics following the two-thirds power law are perceived as more natural than those following a constant velocity—themselves being judged as more natural than those moving according to the shifted two-thirds power law.

Discrimination of targets following or violating biological motion

Previous studies of biological motion have shown that humans are highly sensitive to biological motion perception. However, most studies have focused on the detection of animacy within a body-related framework (typically using point-light displays) (Fox & McDaniel, 1982; Johansson, 1973; Mather & Murdoch, 1994; Neri, Morrone, & Burr, 1998; Pollick et al., 2002; Saygin, Wilson, Hagler, Bates, & Sereno, 2004; Simion et al., 2008). Here, we employed a nonbodily stimulus to remove any structural cue from the display, so the biological motion was implied through kinematic cues only. Furthermore, the task we used involved discriminating the stimulus orientation, so the motion itself was task-irrelevant. Despite these two factors, our results show that participants were consistently faster to report the orientation when the motion kinematics did not follow the two-thirds power law. This difference in discrimination time is in line with either longer target discrimination during biological motion trials (two-thirds power law), more rapid discrimination during trials in which the stimuli movement violated the two-thirds power law, or a combination of both. It is possible that the motion profiles following the two-thirds power law themselves attract attention, thus rendering the discrimination task more difficult in this condition. Indeed, evidence from both human infants and visually unexperienced newborn chicks show longer dwelling times for

Exp.1				
	CFS		Unmasked	
	2/3 power law	Constant velocity	2/3 power law	Constant velocity
RT (Sec)	5.04	5.00	3.55	3.47
SD	1.03	1.04	0.63	0.62
SE	0.24	0.25	0.15	0.15
Exp.2				
	CFS		Unmasked	
	2/3 "shifted"	Constant velocity	2/3 "shifted"	Constant velocity
RT (Sec)	4.52	4.66	3.10	3.22
SD	0.68	0.74	0.40	0.42
SE	0.17	0.18	0.10	0.10
Exp3				
	CFS		Unmasked	
	2/3 power law	2/3 "shifted"	2/3 power law	2/3 "shifted"
RT (Sec)	4.50	4.36	3.30	3.15
SD	0.55	0.51	0.54	0.51
SE	0.13	0.12	0.13	0.12

Table 1. Mean RTs for all experimental conditions.

biological motion, suggesting that such motion may capture attention (Simion et al., 2008; Vallortigara, Regolin, & Marconato, 2005). Alternatively, it is possible that the violation of the two-thirds power law increases the discriminability due to the perceived unnaturalness of the motion stimuli. This is in line with the subjective ratings given by the participants, which indicate that the perceived naturalness of the nonbiological motions were felt to be unnatural. The current results, although indicating a clear difference in the processing of targets moving at or violating biological motion, do not allow us to conclude if this is related to increased saliency for nonbiological motion or some attentional capture or distraction related to the processing of biological motion itself. Further experiments employing visual search paradigms (e.g., Salomon, Lim, Kannape, Llobera, & Blanke, 2013; Yantis & Egeth, 1999) may be useful to disentangle these aspects by allowing the direct testing of differences in saliency as a function of motion type. Interestingly, as the stimuli were presented devoid of any biological movement context, the reason why such deviations from the two-thirds power law were perceived as unnatural remains unknown. It has been suggested that action and perception share common representational coding (Hommel et al., 2001; Knoblich, 2008; Knoblich & Flach, 2001; Prinz, 1990; Schütz-Bosbach & Prinz, 2007). Thus, it is possible that visual motion not adhering to the two-thirds power law is perceived to be unnatural because it violates the underlying motor

invariants of human action (Casile & Giese, 2006; Dayan et al., 2007). Alternatively, it is possible that these nonbiological motion profiles stand out due to the experience and sensitivity of the visual system to biological motion. Thus, these violations of the two-thirds power law may, despite their presence in real-world perception (e.g., car wheel motion), be considered deviant from natural vision statistics, thus increasing their "unnaturalness" and discriminability (Geisler, 2008; Zhang, Tong, Marks, Shan, & Cottrell, 2008). This is in line with previous findings in which atypical visual stimuli have privileged access to awareness (Mudrik et al., 2011) and higher saliency (Loftus & Mackworth, 1978).

Conscious and unconscious processing of biological motion

A secondary aim of this study was to investigate if the processing of the two-thirds power law required explicit attention, which was here manipulated by reducing perceptual awareness through CFS masking. Previous work on biological motion perception has shown that many aspects can be processed relatively automatically (Johansson, 1973; Mather et al., 1992), and others have suggested the involvement of higher level processing requiring attention (Thornton et al., 2002; Thornton & Vuong, 2004). A previous study using point-light walkers masked by CFS found that kinematic but not structural information of biological

motion was processed in the absence of awareness (Faivre & Koch, 2014). The current results show that across all three experiments stimuli following nonbiological motion trajectories were discriminated faster both for masked stimuli as well as for unmasked stimuli. These results support an advantage for perceiving nonbiological stimuli even in the absence of awareness. However, this must be taken with caution as a similar advantage was found for unmasked stimuli, which may indicate that these effects occur after the stimuli enter awareness (see Stein, Hebart, & Sterzer, 2011; Yang, Brascamp, Kang, & Blake, 2014).

Conclusions

The results of this study indicate a behavioral sensitivity for visual motion kinematics following the two-thirds power law. Relying on subjective and objective measures, we found that visual stimuli that did not adhere to the two-thirds power law were judged to be unnatural and were recognized more rapidly even when they were task-irrelevant and outside of any biological context. This supports theories postulating action perception coupling in which visual processing is strongly linked to motor kinematic experience and which has been related to specific cortical systems (Casile et al., 2010; Casile & Giese, 2006; Dayan et al., 2007; Hommel et al., 2001; Knoblich & Flach, 2001; Prinz, 1990; Zwickel, Grosjean, & Prinz, 2010). The current findings extend these previous findings by showing more rapid visual discrimination for nonbiological motions. Further studies may investigate if such cross-modal interactions exist in other modalities, such as tactile and proprioceptive senses.

Keywords: biological motion, two-thirds power law, perceptual consciousness, motor–perception interaction, continuous flash suppression

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References

- Abend, W., Bizzi, E., & Morasso, P. (1982). Human arm trajectory formation. *Brain: A Journal of Neurology*, *105*(Pt. 2), 331–348.
- Ahlström, V., Blake, R., & Ahlström, U. (1997). Perception of biological motion. *Perception*, *26*(12), 1539–1548.
- Beets, I. A. M., Rösler, F., & Fiehler, K. (2010). Nonvisual motor learning improves visual motion perception: Evidence from violating the two-thirds power law. *Journal of Neurophysiology*, *104*(3), 1612–1624.
- Bertenthal, B. I., & Fischer, K. W. (1978). Development of self-recognition in the infant. *Developmental Psychology*, *14*(1), 44–50.
- Bertenthal, B. I., Proffitt, D. R., & Cutting, J. E. (1984). Infant sensitivity to figural coherence in biomechanical motions. *Journal of Experimental Child Psychology*, *37*(2), 213–230.
- Blake, R., & Shiffrar, M. (2007). Perception of human motion. *Annual Review of Psychology*, *58*, 47–73.
- Casile, A., Dayan, E., Caggiano, V., Hendler, T., Flash, T., & Giese, M. A. (2010). Neuronal encoding of human kinematic invariants during action observation. *Cerebral Cortex*, *20*(7), 1647–1655.
- Casile, A., & Giese, M. A. (2006). Nonvisual motor training influences biological motion perception. *Current Biology*, *16*(1), 69–74.
- Cheng, C.-Y., Yen, M.-Y., Lin, H.-Y., Hsia, W.-W., & Hsu, W.-M. (2004). Association of ocular dominance and anisometric myopia. *Investigative Ophthalmology & Visual Science*, *45*(8), 2856–2860. [PubMed] [Article]
- Dayan, E., Casile, A., Levit-Binnun, N., Giese, M. A., Hendler, T., & Flash, T. (2007). Neural representations of kinematic laws of motion: Evidence for action-perception coupling. *Proceedings of the National Academy of Sciences, USA*, *104*(51), 20582–20587.
- de’Sperati, C., & Viviani, P. (1997). The relationship between curvature and velocity in two-dimensional smooth pursuit eye movements. *The Journal of Neuroscience*, *17*(10), 3932–3945.
- Dittrich, W. H. (1993). Action categories and the

- perception of biological motion. *Perception-London*, 22, 15–22.
- Faivre, N., Charron, S., Roux, P., Lehericy, S., & Kouider, S. (2012). Nonconscious emotional processing involve distinct neural pathways for pictures and videos. *Neuropsychologia*, 50(14), 3736–3744.
- Faivre, N., & Koch, C. (2014). Temporal structure coding with and without awareness. *Cognition*, 131(3), 404–414.
- Fox, R., & McDaniel, C. (1982, Oct 29). The perception of biological motion by human infants. *Science*, 218, 486–487.
- Geisler, W. S. (2008). Visual perception and the statistical properties of natural scenes. *Annual Review of Psychology*, 59, 167–192.
- Hiris, E. (2007). Detection of biological and nonbiological motion. *Journal of Vision*, 7(12):4, 1–14, doi:10.1167/7.12.4. [PubMed] [Article]
- Hommel, B., Musseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding (TEC): A framework for perception and action planning. *Behavioral and Brain Sciences*, 24(5), 849–877.
- Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Attention, Perception, & Psychophysics*, 14(2), 201–211.
- Kandel, S., Orliaguet, J.-P., & Viviani, P. (2000). Perceptual anticipation in handwriting: The role of implicit motor competence. *Perception & Psychophysics*, 62(4), 706–716.
- Kaunitz, L., Fracasso, A., Lingnau, A., & Melcher, D. (2013). Non-conscious processing of motion coherence can boost conscious access. *PLoS ONE*, 8(4), e60787.
- Knoblich, G. (2008). Bodily and motor contributions to action perception. *Embodiment, Ego-space, and Action*, 45–78.
- Knoblich, G., & Flach, R. (2001). Predicting the effects of actions: Interactions of perception and action. *Psychological Science*, 12(6), 467–472.
- Lacquaniti, F., Terzuolo, C., & Viviani, P. (1983). The law relating the kinematic and figural aspects of drawing movements. *Acta Psychologica*, 54(1), 115–130.
- Levit-Binnun, N., Schechtman, E., & Flash, T. (2006). On the similarities between the perception and production of elliptical trajectories. *Experimental Brain Research*, 172(4), 533–555.
- Loftus, G. R., & Mackworth, N. H. (1978). Cognitive determinants of fixation location during picture viewing. *Journal of Experimental Psychology: Human Perception and Performance*, 4(4), 565–572.
- Loula, F., Prasad, S., Harber, K., & Shiffrar, M. (2005). Recognizing people from their movement. *Journal of Experimental Psychology: Human Perception and Performance*, 31(1), 210–220.
- Love, J., Selker, R., Marsman, M., Jamil, T., Verhagen, A., & Ly, A. (2015). JASP. (Version 0.6. 6) [Computer software].
- Lupyan, G., & Ward, E. J. (2013). Language can boost otherwise unseen objects into visual awareness. *Proceedings of the National Academy of Sciences, USA*, 110(35), 14196–14201.
- Maruya, K., Yang, E., & Blake, R. (2007). Voluntary action influences visual competition. *Psychological Science*, 18(12), 1090–1098.
- Mather, G., & Murdoch, L. (1994). Gender discrimination in biological motion displays based on dynamic cues. *Proceedings of the Royal Society of London B: Biological Sciences*, 258(1353), 273–279.
- Mather, G., Radford, K., & West, S. (1992). Low-level visual processing of biological motion. *Proceedings of the Royal Society of London B: Biological Sciences*, 249(1325), 149–155.
- Mudrik, L., Breska, A., Lamy, D., & Deouell, L. Y. (2011). Integration without awareness. *Psychological Science*, 22(6), 764–770.
- Neri, P., Morrone, M. C., & Burr, D. C. (1998, Oct 29). Seeing biological motion. *Nature*, 395, 894–896.
- Papaxanthis, C., Paizis, C., White, O., Pozzo, T., & Stucchi, N. (2012). The relation between geometry and time in mental actions. *PLoS One*, 7(11), e51191, doi:10.1371/journal.pone.0051161.
- Perrier, P., & Fuchs, S. (2008). Speed–curvature relations in speech production challenge the 1/3 power law. *Journal of Neurophysiology*, 100(3), 1171–1183.
- Pham, Q. C., Hicheur, H., Arechavaleta, G., Laumond, J. P., & Berthoz, A. (2007). The formation of trajectories during goal-oriented locomotion in humans. II. A maximum smoothness model. *European Journal of Neuroscience*, 26(8), 2391–2403.
- Pollick, F. E., Lestou, V., Ryu, J., & Cho, S.-B. (2002). Estimating the efficiency of recognizing gender and affect from biological motion. *Vision Research*, 42(20), 2345–2355.
- Prinz, W. (1990). *A common coding approach to perception and action*. Berlin Heidelberg: Springer.
- Salomon, R., Galli, G., Łukowska, M., Faivre, N., Ruiz, J. B., & Blanke, O. (2015). An invisible touch: Body-related multisensory conflicts modulate visual consciousness. *Neuropsychologia*, epub ahead of print, doi:10.1016/j.neuropsychologia.2015.10.034.

- Salomon, R., Kaliuzhna, M., Herbelin, B., & Blanke, O. (2015). Balancing awareness: Vestibular signals modulate visual consciousness in the absence of awareness. *Consciousness and Cognition*, *36*, 289–297.
- Salomon, R., Lim, M., Herbelin, B., Hesselmann, G., & Blanke, O. (2013). Posing for awareness: Proprioception modulates access to visual consciousness in a continuous flash suppression task. *Journal of Vision*, *13*(7):2, 1–8, doi:10.1167/13.7.2. [PubMed] [Article]
- Salomon, R., Lim, M., Kannape, O., Llobera, J., & Blanke, O. (2013). “Self pop-out”: Agency enhances self-recognition in visual search. *Experimental Brain Research*, *228*(2), 173–181.
- Saygin, A. P., Wilson, S. M., Hagler, D. J., Bates, E., & Sereno, M. I. (2004). Point-light biological motion perception activates human premotor cortex. *The Journal of Neuroscience*, *24*(27), 6181–6188.
- Schütz-Bosbach, S., & Prinz, W. (2007). Perceptual resonance: Action-induced modulation of perception. *Trends in Cognitive Sciences*, *11*(8), 349–355.
- Simion, F., Regolin, L., & Bulf, H. (2008). A predisposition for biological motion in the newborn baby. *Proceedings of the National Academy of Sciences, USA*, *105*(2), 809–813.
- Soechting, J., Lacquaniti, F., & Terzuolo, C. (1986). Coordination of arm movements in three-dimensional space. Sensorimotor mapping during drawing movement. *Neuroscience*, *17*(2), 295–311.
- Stein, T., Hebart, M. N., & Sterzer, P. (2011). Breaking continuous flash suppression: A new measure of unconscious processing during interocular suppression? *Frontiers in Human Neuroscience*, *5*, 167.
- Tasko, S. M., & Westbury, J. R. (2004). Speed–curvature relations for speech-related articulatory movement. *Journal of Phonetics*, *32*(1), 65–80.
- Thompson, J., & Parasuraman, R. (2012). Attention, biological motion, and action recognition. *Neuroimage*, *59*(1), 4–13.
- Thornton, I. M., Rensink, R. A., & Shiffrar, M. (2002). Active versus passive processing of biological motion. *Perception-London*, *31*(7), 837–854.
- Thornton, I. M., & Vuong, Q. C. (2004). Incidental processing of biological motion. *Current Biology*, *14*(12), 1084–1089.
- Troje, N. F., Westhoff, C., & Lavrov, M. (2005). Person identification from biological motion: Effects of structural and kinematic cues. *Perception & Psychophysics*, *67*(4), 667–675.
- Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience*, *8*(8), 1096–1101.
- Vallortigara, G., Regolin, L., & Marconato, F. (2005). Visually inexperienced chicks exhibit spontaneous preference for biological motion patterns. *PLoS Biology*, *3*(7), e208.
- Vieilledent, S., Kerlirzin, Y., Dalbera, S., & Berthoz, A. (2001). Relationship between velocity and curvature of a human locomotor trajectory. *Neuroscience Letters*, *305*(1), 65–69.
- Viviani, P., Baud-Bovy, G., & Redolfi, M. (1997). Perceiving and tracking kinesthetic stimuli: Further evidence of motor–perceptual interactions. *Journal of Experimental Psychology: Human Perception and Performance*, *23*(4), 1232–1252.
- Viviani, P., & Flash, T. (1995). Minimum-jerk, two-thirds power law, and isochrony: Converging approaches to movement planning. *Journal of Experimental Psychology: Human Perception and Performance*, *21*(1), 32–53.
- Viviani, P., & Stucchi, N. (1992). Biological movements look uniform: Evidence of motor–perceptual interactions. *Journal of Experimental Psychology: Human Perception and Performance*, *18*(3), 603–623.
- Viviani, P., & Terzuolo, C. (1982). Trajectory determines movement dynamics. *Neuroscience*, *7*(2), 431–437.
- Yang, E., Brascamp, J., Kang, M.-S., & Blake, R. (2014). On the use of continuous flash suppression for the study of visual processing outside of awareness. *Frontiers in Psychology*, *5*, 724, doi:10.3389/fpsyg.2014.00724.
- Yantis, S., & Egeth, H. (1999). On the distinction between visual salience and stimulus-driven attentional capture. *Journal of Experimental Psychology: Human Perception and Performance*, *25*(3), 661–676.
- Zhang, L., Tong, M. H., Marks, T. K., Shan, H., & Cottrell, G. W. (2008). SUN: A Bayesian framework for saliency using natural statistics. *Journal of Vision*, *8*(7):32, 1–20, doi:10.1167/8.7.32. [PubMed] [Article]
- Zwicker, J., Grosjean, M., & Prinz, W. (2010). On interference effects in concurrent perception and action. *Psychological Research*, *74*(2), 152–171.