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Kinesthesis Can Make an Invisible Hand Visible

Kevin C. Dieter[1,2], Bo Hu[2], David C. Knill[1,2], Randolph Blake[3,4,5], and Duje Tadin[1,2,6]

[1]Department of Brain and Cognitive Sciences, University of Rochester; [2]Center for Visual Science, University of Rochester; [3]Department of Brain and Cognitive Sciences, Seoul National University; [4]Vanderbilt Vision Research Center, Vanderbilt University; [5]Department of Psychological Sciences, Vanderbilt University; and [6]Department of Ophthalmology, University of Rochester School of Medicine

Abstract

Self-generated body movements have reliable visual consequences. This predictive association between vision and action likely underlies modulatory effects of action on visual processing. However, it is unknown whether actions can have generative effects on visual perception. We asked whether, in total darkness, self-generated body movements are sufficient to evoke normally concomitant visual perceptions. Using a deceptive experimental design, we discovered that waving one's own hand in front of one's covered eyes can cause visual sensations of motion. Conjecturing that these visual sensations arise from multisensory connectivity, we showed that grapheme-color synesthetes experience substantially stronger kinesthesis-induced visual sensations than nonsynesthetes do. Finally, we found that the perceived vividness of kinesthesis-induced visual sensations predicted participants' ability to smoothly track self-generated hand movements with their eyes in darkness, which indicates that these sensations function like typical retinally driven visual sensations. Evidently, even in the complete absence of external visual input, the brain predicts visual consequences of actions.

Keywords

multisensory perception, visual motion perception, kinesthesis, synesthesia, predictive coding, perception, vision, motor processes, motion perception

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Self-generated movements evoke a variety of sensory signals, ranging from proprioceptive to visual sensations. Typically, the evoked sensory signals reliably co-occur with one another and with the body movements that trigger them. This predictive relationship between action and perception underlies a number of brain functions. For example, the efference signals associated with one's actions enable improved estimation of body states (Wolpert, Ghahramani, & Jordan, 1995) and compensation of pervasive sensory delays, which allows predictive control of dynamic motor behaviors (Flanagan & Wing, 1997). Efference signals can also alter perception—self-generated tactile stimuli, such as tickling, are felt less strongly than equivalent externally generated signals (Blakemore, Frith, & Wolpert, 1999).

One's actions also have reliable visual consequences—a fact dramatically illustrated by Ian Waterman, who learned to use vision to compensate for a total loss of proprioception (Cole, 1995). Empirical evidence shows that self-generated movements can modulate visual processing (Christensen, Ilg, & Giese, 2011; Davies, 1973; Hu & Knill, 2010; Lally, Frendo, & Diedrichsen, 2011; Maruya, Yang, & Blake, 2007; Salomon, Lim, Herbelin, Hesselmann, & Blanke, 2013). Moreover, the interplay between vision and kinesthesis is critical to how people perceive their bodies. Sensations as fundamental as one's sense of body location can be overridden by misaligning visual and proprioceptive inputs (Botvinick & Cohen, 1998; Ehrsson, 2007). This ability of vision to influence proprioception is exploited in mirror-box therapy for

Corresponding Author:
Duje Tadin, University of Rochester, Department of Brain and Cognitive Sciences, Meliora Hall 318, Rochester, NY 14627
E-mail: duje@cvs.rochester.edu

patients with phantom limbs (Ramachandran & Rogers-Ramachandran, 1996). These proprioception-vision interactions seem to depend on a history of consistent multisensory pairings; such effects are largely absent in young children (Gori, Del Viva, Sandini, & Burr, 2008) and in individuals born without arms (Funk, Shiffrar, & Brugger, 2005).

It remains unknown, however, whether the visual effects of action are limited to modulations or extend to stronger, generative effects. In the experiments reported here, our broad aim was to determine whether a stimulus that is strongly predictive of a perceptual response in another sensory modality might itself evoke that perceptual response. This approach is analogous to that used to reveal predictive associations in classical conditioning (Pavlov, 1927). Specifically, we asked whether, in the complete absence of external visual input, self-generated body movements are solely sufficient to cause visual perceptual experiences ordinarily accompanying those movements. We conducted a series of subjective-rating experiments to establish whether, and under what conditions, participants naive to the purpose of the experiments would report experiencing kinesthesis-induced visual sensations. To provide an objective measure of these sensations, we also conducted an eye-tracking experiment to test whether the reported illusory visual sensations of motion could function similar to genuine, retinally driven visual motion signals.

Method

Participants

We recruited 129 participants (46 male, 83 female) to participate in five experiments. All were naive to the purpose of the experiments, and, unless noted, each individual participated in only one experiment. The institutional review boards at the University of Rochester and at Vanderbilt University approved all procedures for tests performed at those sites.

Experiment 1: self-motion. Forty-nine participants (17 male, 32 female) completed this experiment. We found a tendency for males to show stronger results than females (p = .015); this tendency parallels previous findings of gender differences in visual-haptic tasks (Linn & Petersen, 1985). We controlled for the mismatch in sample sizes across genders by, first, computing frequency histograms separately for the two genders and then averaging; that is, we weighted male and female results equally. For relevant nonparametric analyses, we created a representative subsample of 17 female individuals whose frequency histogram best matched the full female sample (means within 1.4%; identical medians, minimums, maximums, and first quartiles; the third quartile was 0.25 smaller in the new sample). We then combined these individuals with male participants, so that there were 34 participants total.

During experimental trials, participants wore tightly fitting blindfolds (Mindfold, Durango, CO) and made visual judgments while freely waving their own hand back and forth in front of their eyes at a slow, comfortable pace (Fig. 1a). To encourage uniform hand waving across all participants, the experimenter began each session by demonstrating the action that was to be executed. The same experimenter tested almost all participants (> 98%), so this exemplar hand wave was largely uniform.

Deception. The experimental design involved two aspects of deception designed to induce experimentally controlled expectations. First, participants (tested individually) were told that we were investigating “visual sensitivity to motion under low lighting conditions.” Second, they were shown two functionally identical blindfolds that appeared different: One was unaltered, whereas the other had several dozen small holelike indentations. Although both blindfolds blocked all light, participants were told that only the first blindfold would block “all light,” whereas the other “may allow a small amount of light to pass through” and that they “may or may not perceive anything differently while wearing this blindfold.” Thus, participants were explicitly led to expect no visual sensation with one blindfold and to expect that they might see something while wearing the other (Table 1).

On each trial, participants wore one of the blindfolds—selected at random without replacement—and were asked to execute self-generated hand movements (Fig. 1a) and to note accompanying visual sensations, if any. Participants were not told which blindfold was worn on which trial. Therefore, on Trial 1, participants should consider it possible, though not necessarily likely, that they might have a visual experience. Expectations on Trial 2 would depend on visual sensations experienced on Trial 1 (Table 1). Specifically, seeing something on Trial 1 created an expectation of seeing nothing on Trial 2 (but not necessarily vice versa if no visual sensation was experienced on Trial 1). From participant debriefing, we found that this approach was conservative in assessing the incidence and the strength of kinesthesis-induced visual sensations.

Procedure. To conceal the fact that the holelike indentations did not break the surface of the blindfold and to prevent participants from feeling the indentations, we placed cardboard pieces with adhesive backing on the front of both blindfolds. The two blindfolds were shuffled in front of each participant while his or her eyes were closed. The participant then selected one of the

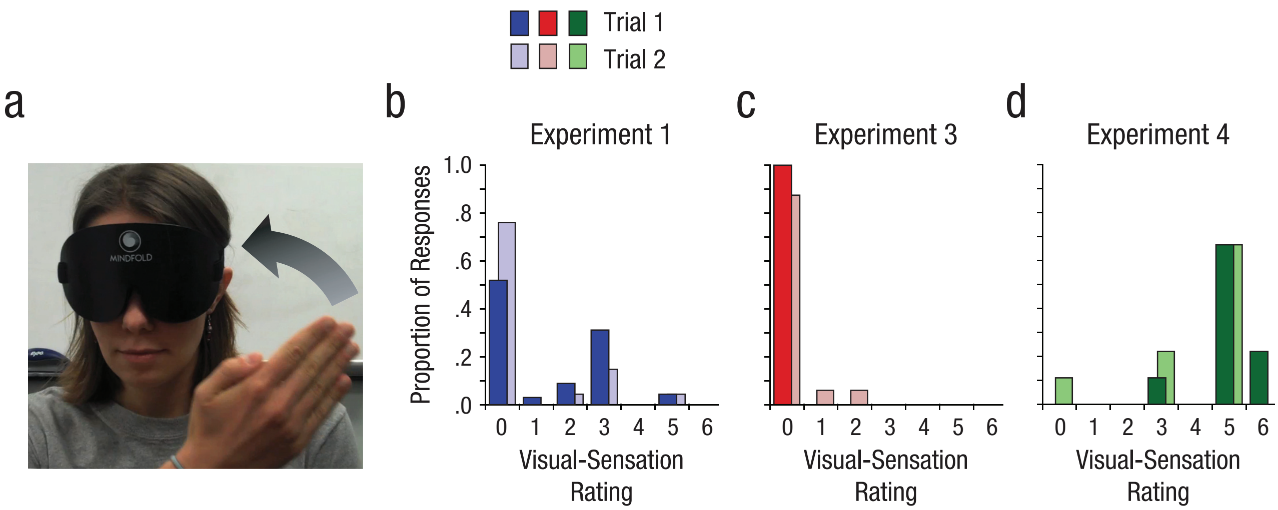

Fig. 1. Illustration of the paradigm used in Experiments 1 through 4 (a) and results from Experiments 1, 3, and 4 (b–d, respectively). Participants were blindfolded and, in Experiments 1, 2, and 4, asked to wave their hand back and forth in front of the blindfold at a slow, comfortable pace, as shown here. In Experiment 3, the experimenter waved his hand in front of participants' faces in the same manner. Participants rated their accompanying visual sensations on a scale with 0 (*no visual sensation at all*) to 6 (*the visual shape looked like the outline of a moving hand*) as anchors and 3 (*visual sensation of motion with direction*) as the key target response. The histograms show the proportion of responses for each point on the visual-sensation scale in Trials 1 and 2 of Experiments 1, 3, and 4.

blindfolds and put it on. Once the blindfold was secure, the experimenter removed the stickers and asked the participant to open his or her eyes. This procedure was strictly followed.[1] Next, the experimenter verbally administered the Edinburgh Handedness Inventory (Oldfield, 1971). Each participant was randomly assigned to use his or her dominant or nondominant hand in the experiment. We found no effect of hand dominance (p = .92), so these data were combined.

Participants were told that they would make a visual-sensation rating at the end of each trial and to keep waving their hand in front of their eyes until they were ready. Once they indicated their readiness to make a rating, the experimenter administered a sequential questionnaire (participants had previously been familiarized with all questions). Each question required a simple "yes" or "no" response. If the participant answered "no," the questionnaire ended. The following sequence of questions was asked:

1. Would you say that you had any visual sensation at all?
2. Would you say that you had a visual sensation of motion?
3. Would you say that you had a visual sensation of motion with direction?
4. Would you say that the motion that you saw had any discernible shape or form?
5. Would you say that the visual shape was vertically elongated, taller than it is wide?
6. Would you say that the visual shape looked like the outline of a moving hand?

Table 1. Experimentally Induced Expectations in Experiments 1, 3, and 4

Trial	Had a visual sensation on Trial 1	Expected blindfold	Expected chance of experiencing a visual sensation
Trial 1	—	Both equally likely	Low
Trial 2	No	Probably the "leaky" blindfold	Maybe
	Yes	The unaltered blindfold	None

Note: Utilizing deceptive instructions, we experimentally controlled participants' expectations by showing them two blindfolds, an unaltered one and a "leaky" one that appeared to have small holes in it (but did not). These instructions led participants to believe that it was possible, though not necessarily likely, that they might experience a visual sensation on Trial 1. Their expectation in Trial 2 depended on their actual visual experience in Trial 1. See the Method section for additional details.

Participants were given a score from 0 to 6. A score of 1 through 6 corresponded to the last question to which they answered "yes," and they received a score of 0 if they answered "no" to the first question. Participants sometimes expressed uncertainty when answering. In these cases, the experimenter disinterestedly reminded the participant that he or she must make a "yes" or "no" decision. After completing both trials, participants completed the Vividness of Visual Imagery Questionnaire (Marks, 1973). Finally, participants were debriefed and told the true purpose of the experiment.

Experiment 2: self-motion, blindfold selection with replacement. Twenty participants (10 male, 10 female) completed this experiment. This experiment was identical to Experiment 1, except that, on each trial, the blindfold was selected randomly with replacement. Participants were explicitly told that the chances were 50/50 that they might receive the same blindfold on both trials.

Experiment 3: experimenter motion. Sixteen participants (8 male, 8 female) completed this experiment. The experimenter sat opposite the participant and waved his hand back and forth at the exemplar pace, saying "left" and "right" when reaching movement endpoints. We provided verbal cues to participants to ensure that stimulus timing was the same as in the previous experiments. Other than the change from self to experimenter motion, the methodology was the same as in Experiment 1.

Experiment 4: self-motion, participants with synesthesia. What causes the visual sensations experienced during self-generated hand movement? The perceptual reality of these reported sensations presumably requires functional connectivity between kinesthetic and proprioceptive areas, on the one hand, and brain areas capable of generating visual sensations, on the other. Additionally, it is likely that the strength of such cross-modally generated sensations would depend on cortical excitability (Bolognini, Senna, Maravita, Pascual-Leone, & Merabet, 2010; Ramos-Estebanez et al., 2007). These considerations led us to wonder whether individuals with greater cortical connectivity and excitability would experience stronger kinesthesis-induced visual sensations. To pursue this possibility, we recruited individuals for Experiment 4 who had grapheme-color synesthesia, a condition defined by strong associations between sensory modalities or submodalities. Whereas synesthesia is usually studied in the context of self-reported synesthetic pairings, experimental evidence links synesthesia with global changes in neural processing (Barnett et al., 2008), including both increased connectivity (Hänggi, Wotruba, & Jäncke, 2011; Rouw & Scholte, 2007) and enhanced cortical excitability (Terhune, Tai, Cowey, Popescu, & Cohen Kadosh, 2011). The existence of such global changes suggests the possibility of an even broader range of unique cross-sensory experiences in individuals with synesthesia.

This experiment was identical to Experiment 1, except that participants (N = 9, 1 male, 8 female) were grapheme-color synesthetes. All participants self-reported their synesthetic experiences, and most completed an online battery to confirm these self-reports (Eagleman, Kagan, Nelson, Sagaram, & Sarma, 2007). Seven synesthetes were associators, with one projector, and one who experienced both. No synesthete reported visuo-proprioceptive synesthesia.

Experiment 5: eye tracking. Finally, we asked whether kinesthesis-induced visual sensations of motion could mimic the effects of retinally driven visual motion. To answer this question, we turned to smooth pursuit eye movements, a function dependent on visual motion signals (Kowler, 2011). Although it is possible for the eyes to follow self-generated movements in total darkness, the smoothness of such eye movements is greatly reduced (Berryhill, Chiu, & Hughes, 2006; Watanabe & Shimojo, 1997). In fact, previous investigations have revealed considerable individual variability in participants' visual pursuit of self-generated movements in total darkness (Glenny & Heywood, 1979; Jordan, 1970; Watanabe & Shimojo, 1997). We hypothesized that this variability may be, at least in part, due to individual differences in the quality of visual sensations caused by self-movement. Specifically, we predicted that individuals who experience more vivid kinesthesis-induced visual sensations would exhibit smoother eye tracking of their hand motion in complete darkness. The assumption was that illusory visual sensations of hand motion would provide a "lock" for smooth pursuit eye movements, essentially functioning as retinally driven motion sensations.

Twenty nonsynesthetes (10 male, 10 female) and 6 synesthetes (all female) participated in this experiment. Two synesthetes, who also participated in Experiment 4, experienced grapheme-color associations. Other synesthetes reported the following associations: weekdays/months-space, sound-taste, grapheme-personality, weekdays/months-color, pitch/chords-color, number-gender/personality. In a totally dark room, each participant completed three hand-motion conditions (self-motion, experimenter motion, and silhouette motion) under two eye-movement conditions (fixation and pursuit). The resulting six conditions, each consisting of three trials, were counterbalanced. The self- and experimenter-motion conditions were the same as in Experiments 1 and 3, respectively. In the silhouette-motion condition, participants waved a cardboard silhouette of an arm (46 cm in length) so that the hand portion (21 cm) passed in front of their eyes. In the fixation conditions, participants were told to look straight ahead. In the pursuit conditions, participants were instructed to follow the movement of the hand with their eyes. Following the explanation of these conditions, participants practiced (three trials) visually pursuing their own hand in a lit room. Next, participants were familiarized with the following statements:

- During the experiment, there were times when I had a visual sensation.
- During the experiment, there were times when I had a visual sensation of motion.
- During the experiment, there were times when I had a visual sensation of color.
- During the experiment, there were times when I had a visual sensation of a moving form.
- During the experiment, there were times when I had a visual sensation of the outline of a hand.
- During the experiment, there were times when I visually perceived individual fingers.
- During the experiment, there were times when I visually perceived other objects in the room.

After each trial, participants rated their disagreement or agreement with each statement on a 7-point Likert scale. Some statements were of experimental interest, and some (e.g., "perceived other objects in the room") were control statements.

Eye position was tracked using a head-mounted eye tracker (EyeLink II, SR Research, Kanata, Ontario, Canada). To ensure complete darkness, we fitted 900-925-nanometer illuminators with high-pass infrared filters whose efficacy was confirmed by dark-adapted observers. Eye-tracking analysis was based on data from 20 out of 26 participants (for 6 participants, including 1 synesthete, eye position recordings were corrupted). Following eye calibration (repeated at the beginning of each condition), the computer monitor and all lights were turned off. Participants were instructed to indicate when the monitor afterimage had completely faded. Thirty seconds later, a computer voice informed the participant (or the experimenter) to initiate hand waving. Each trial lasted 10 s. The three trials in each condition were separated by 5-s breaks.

Eye position data (sampled at 250 Hz) were first smoothed with a 75-ms median filter and then with a 75-ms, third-order Savitzky-Golay filter; high-frequency variations were smoothed without flattening eye position. These position traces were differentiated to yield eye velocity. Saccades were defined by polar eye velocity that was 20° per second higher than median velocity over a sliding ±64-ms window and were confirmed manually. Smoothness of ocular pursuit was assessed using pursuit component gain, computed as the proportion of the total distance traveled by the eye on a given trial that was accounted for by smooth pursuit eye movements (Gregory, 1958; Watanabe & Shimojo, 1997). This metric ranged from 0, indicating only saccadic eye movements, to 1, indicating that only pursuit eye movements occurred.

Results[2]

Experiment 1: self-motion

In our main experiment, the majority of participants reported experiencing visual sensations while waving their hand (Fig. 1b). On Trial 1, approximately 50% of participants reported visual sensations, most commonly a "visual sensation of motion," described during debriefing as a moving shadow or darkening. On Trial 2, participants who reported visual sensations on Trial 1 would be explicitly biased against a second positive report. Although this explicit bias to report no visual sensation did result in weaker overall ratings on Trial 2 (z = 2.26, p = .02), 44% of participants who reported visual sensations on Trial 1 also reported visual sensations on Trial 2. Moreover, all but 1 participant who reported visual sensations on Trial 2 had reported sensations on Trial 1—an observation that is unequivocally inconsistent with our deceptive instructions but is consistent with the perceptual reality of the reported sensations. It is notable that these ratings did not correlate with participants' visual-imagery ability (rs = −.07 and −.02 for Trial 1 and Trial 2, respectively; all ps > .67), which argues against a significant role of visual imagery in the observed results.

Experiment 2: self-motion, blindfold selection with replacement

In Experiment 2, participants were aware that they might select the same blindfold two trials in a row, effectively eliminating differences in expectations on Trial 1 and Trial 2. Results indeed showed that the incidence of seeing motion did not differ between the two trials (z = 0.32, p = .75). In addition, ratings did not differ from Trial 1 ratings in Experiment 1 (z = −0.92, p = .37).

Experiment 3: experimenter motion

In Experiment 3, the experimenter waved his hand in front of the blindfold, but all other details were the same as in Experiment 1. Under these conditions, no participant reported visual sensations on Trial 1 (Fig. 1c). Visual sensations were significantly weaker than those in both Trial 1 and 2 of Experiment 1 (z = 3.22, 2.07; p = .001, .038, respectively) and significantly weaker than those in Experiment 2 (z = 2.33, p = .020). Moreover, in Experiment 3, only 2 out of the 16 participants gave positive reports on Trial 2 (Fig. 1c). Overall, these results highlight the key role of self-generated movement in the visual sensations reported in Experiments 1 and 2.

Experiment 4: self-motion, participants with synesthesia

Repeating Experiment 1 with grapheme-color synesthetes, visual sensations were reported to be substantially stronger than in the initial experiment (Fig. 1d). On Trial 1, all synesthetes reported experiencing visual perceptions, and these were considerably stronger than those of nonsynesthetes ($z = 4.38$, $p = 10^{-5}$). Nearly all synesthetes reported perceiving visual form in addition to visual motion. Additionally, Trial 2 ratings for synesthetes did not differ significantly from those on Trial 1 ($p = .25$), even though these individuals were led to expect to see nothing on at least one of the two trials. During debriefing, synesthetes typically described their visual experiences as resembling an inverted pendulum or a well-defined moving dark bar. Synesthetic participants did not significantly differ from nonsynesthetic participants in their ability to generate visual imagery ($z = -0.76$, $p = .45$). Along with a lack of significant correlation between visual imagery and Experiment 1 ratings, this result further argues against the alternative explanation that participants were merely using mental imagery to visualize reported hand motion.

Experiment 5: eye tracking

In this final experiment, there were three types of "hand" motion: self-motion, silhouette motion, and experimenter motion. These conditions were performed while participants either fixated straight ahead or tried to visually pursue the moving hand. First, to assess the vividness of experienced visual sensations, we obtained Likert-scale ratings for all six conditions (Fig. 2). A three-way analysis of variance revealed main effects of motion type, $F(2, 50) = 19.6$, $p < 10^{-6}$, and rating, $F(6, 150) = 49.5$, $p < 10^{-6}$. We also found an interaction between motion type and rating, $F(12, 300) = 4.8$, $p < 10^{-6}$, which was largely driven by stronger visual motion and form sensations in the self-motion and silhouette-motion conditions than in the experimenter-motion condition (Fig. 2). Ratings were marginally higher in the fixation condition than in the pursuit condition, $F(1, 25) = 3.6$, $p = .069$. This result is consistent with debriefing reports, which indicated that visual sensations were stronger when a participant's hand was moving in the visual periphery than in the foveal area. In particular, in the fixation condition, higher ratings for the visual sensation, motion, and moving-form questions (Questions 1, 2, and 4) than for the other questions drove an interaction between rating and eye-movement condition, $F(6, 150) = 3.5$, $p = .003$. Relatively similar ratings for the self-motion and silhouette-motion conditions suggest that experienced sensations may also extend to handheld objects (Carlson, Alvarez, Wu, & Verstraten, 2010). As in the previous experiment, there was a tendency for synesthetes to report stronger ratings than nonsynesthetes, but this effect was much weaker in the present experiment (a median increase of one response on the Likert scale)—a result likely reflecting greater heterogeneity of synesthesia types in this experiment. We also observed considerable individual differences in reported

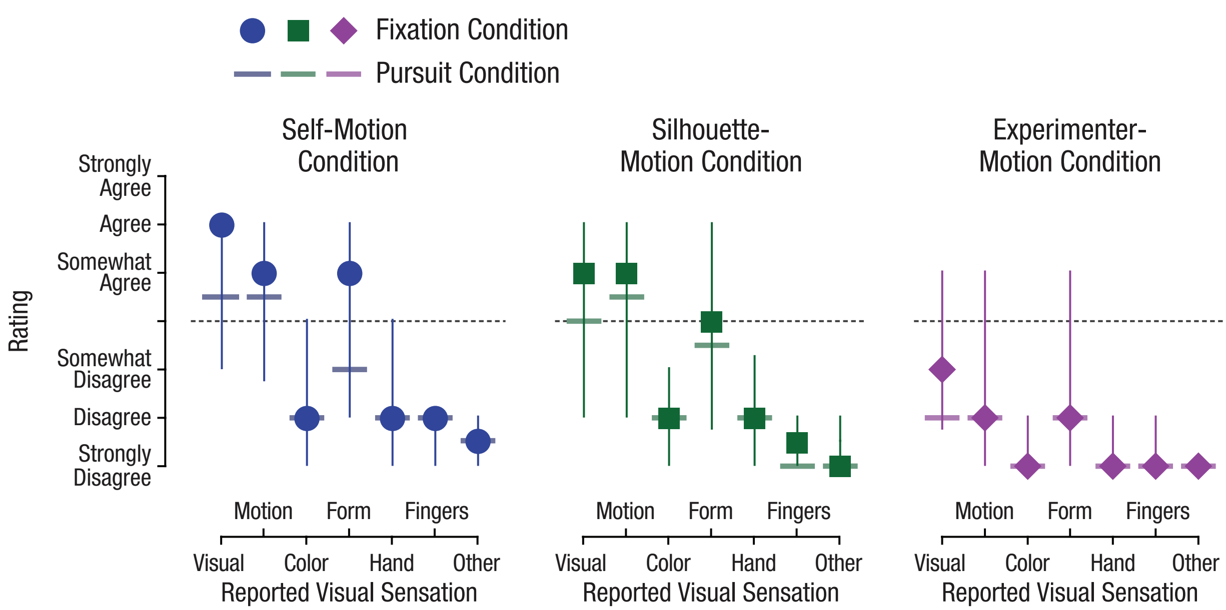

Fig. 2. Median rating on seven items measuring visual perception in Experiment 5 as a function of eye-movement condition. Results are shown separately for the self-, silhouette-, and experimenter-motion conditions. See the Method for descriptions of the scale items. Vertical lines indicate the interquartile range for data from the fixation condition. Dashed horizontal lines indicate the neutral response (*neither agree nor disagree*).

visual ratings, which allowed us to test whether this variability predicts the smoothness of eye movements.

The extent to which individuals smoothly tracked their hand in total darkness was assessed by pursuit component gain (Gregory, 1958; Watanabe & Shimojo, 1997). This metric quantifies the proportion of the total angular distance that is smoothly traversed by the eye. As expected (Berryhill et al., 2006; Jordan, 1970; Watanabe & Shimojo, 1997), motion type affected pursuit smoothness (Fig. 3a), $F(2, 38) = 12.3$, $p < 10^{-4}$, with smoother pursuit in the self- and silhouette-motion conditions than in the experimenter-motion condition. Confirming our hypothesis, results showed that pursuit component gain was predicted by visual-sensation ratings. Specifically, participants who, in the self-motion condition, described experiencing visual sensations of form and motion tended to make significantly smoother eye movements in darkness than participants who did not describe these sensations (Fig. 3b). Similar results were found when we excluded participants with synesthesia (all ps < .02). Figure 4a shows eye traces whose pursuit component gains best matched the data in Figure 3b. Evidently, affirmative visual-sensation ratings are associated with noticeably smoother pursuit eye movements than negative visual-sensation ratings are. As an extreme example, 1 synesthetic participant reported vivid kinesthesis-induced visual sensations and exhibited nearly perfect smooth pursuit in total darkness (see Fig. 4b).

Supporting the results shown in Figure 4b, we found significant correlations between pursuit component gain during self-motion and vividness ratings of accompanying visual sensation (r = .60), visual motion (r = .59), moving form (r = .50), and hand outline (r = .46; all ps < .04). Other ratings were uncorrelated with pursuit component gain (all ps > .11). In the silhouette-motion condition, we found trends between pursuit component gain and ratings of visual sensation (r = .42, p = .065) and visual motion (r = .43, p = .058). No correlations were found in the experimenter-motion condition (all ps > .14).

Discussion

Our findings indicate that action-vision interactions go beyond cross-sensory modulations—kinesthesis can actually generate visual sensations. Executing hand movements in a way that normally results in retinally driven visual experiences can be solely sufficient to generate corresponding visual perceptions. This finding reveals a rather basic effect of action on visual processing. Such effects are almost certainly advantageous, as, in essence, action provides advance information about visual signals caused by self-movement. Depending on task demands, this information could be used to either suppress (Lally et al., 2011) or enhance (Christensen et al., 2011) visual processing. Visual perceptions caused by self-movement could be derived from two separate

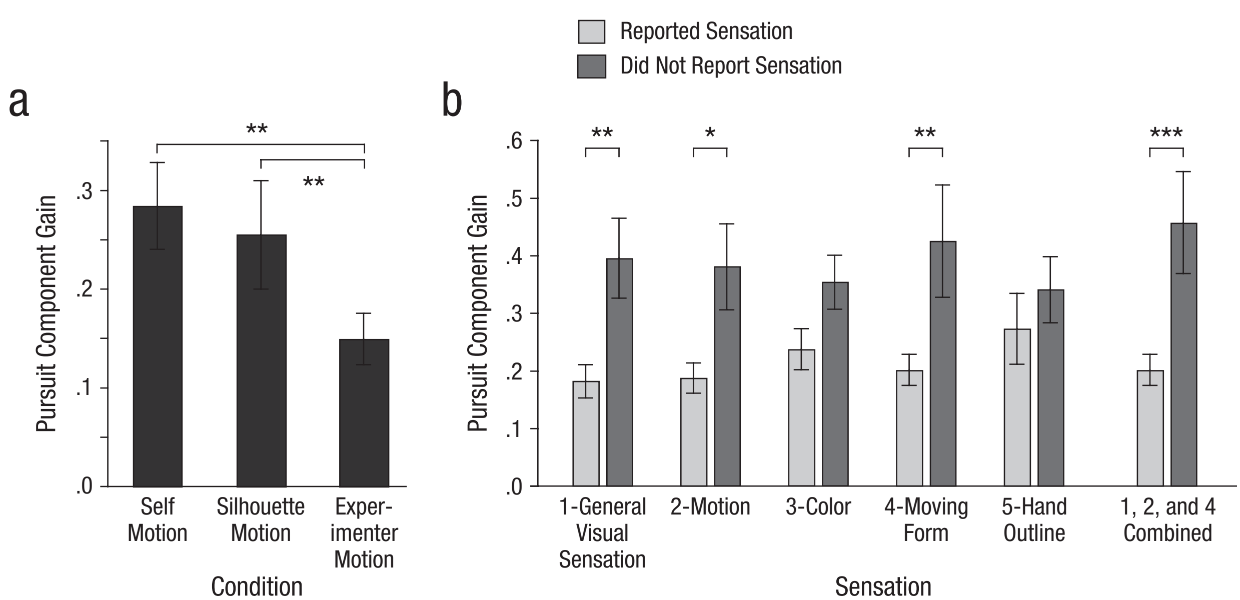

Fig. 3. Mean pursuit component gain in Experiment 5 as a function of (a) motion condition and (b) reported sensation in the self-motion condition. Results are shown in (b) only for rating questions that had more than three affirmative answers; for those questions, participants were split into those reporting visual sensations and those responding negatively (i.e., "agree" vs. "disagree" responses, respectively; see the Method for descriptions of the scale items). Pursuit component gain was the proportion of the total distance on a given trial smoothly traversed by the eye. Asterisks indicate significant differences between conditions (*p < .05, **p < .01, ***p < .001). Error bars show standard errors of the mean.

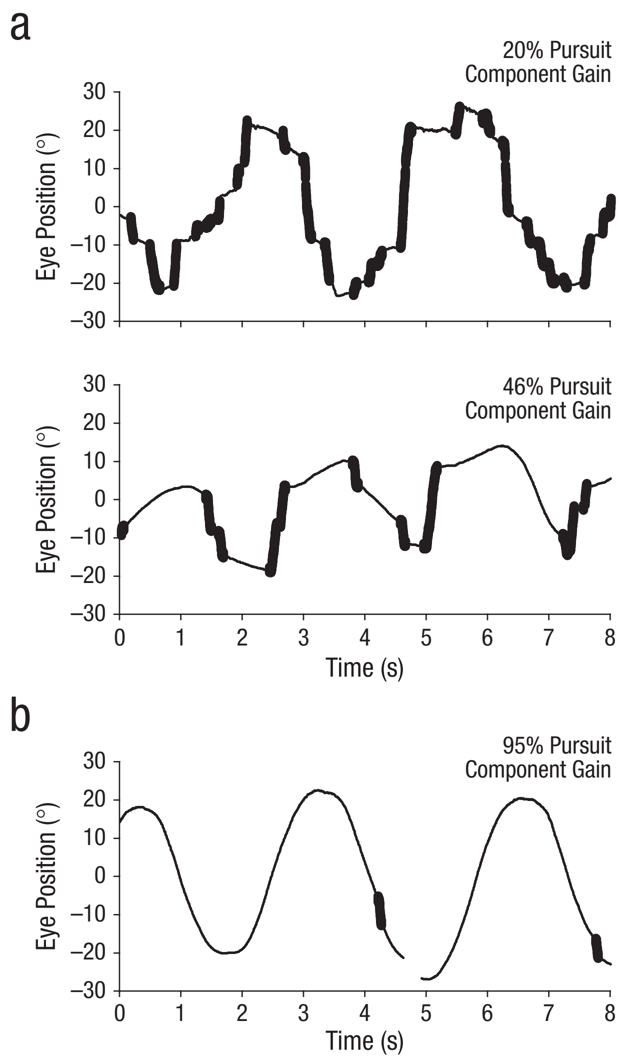

Fig. 4. Representative horizontal eye position traces from the self-motion condition in Experiment 5. The graphs in (a) show two individual trials that best matched the pursuit component gains for the combined results of the visual-sensation, motion, and form questions (right-most bars in Fig. 3b). Boldface indicates eye positions that comprised saccades, and thin lines indicate smooth pursuit eye movements. The top trace illustrates 20% pursuit component gain, which corresponds to the average pursuit component gain for participants that had median ratings in the "disagree" range. The bottom trace shows 46% pursuit component gain, which corresponds to the average pursuit component gain for participants whose ratings were in the "agree" range. The graph in (b) shows results for a synesthetic participant who exhibited near-perfect smooth pursuit of self-motion in total darkness.

but related sources. They could be based on the efference copy associated with relevant motor commands (Bays & Wolpert, 2007), or, alternatively, the proprioceptive sensory feedback itself could represent the signals evoking visual sensations. Our results do not allow us to distinguish between these two possibilities. Although the efference copy has long been associated with predictive coding, there are also numerous reports of interactions between proprioception and vision.

Although our results support the hypothesis that action can generate visual sensations, we found considerable individual variability in reported sensations. Some individuals confidently reported no visual sensations, whereas others described seeing well-defined visual forms. Within this latter group were individuals with synesthesia, which suggests that sensory interconnectivity (Hänggi et al., 2011; Rouw & Scholte, 2007), cortical excitability (Terhune, et al., 2011), or both factors might play a role in kinesthesis-induced visual perceptions. It is reasonable to assume that increased functional connectivity between proprioceptive-kinesthetic regions and brain areas capable of generating visual percepts would result in increased influence of kinesthesis over visual processing. Additionally, increased excitability of occipital cortex in grapheme-color synesthesia (Terhune et al., 2011) may contribute to the perceptual visibility of weak inputs to visual areas (Ramos-Estebanez et al., 2007; Romei, Murray, Cappe, & Thut, 2009). Although the underlying causes of synesthesia are still debatable (Bargary & Mitchell, 2008; Robertson & Sagiv, 2005), our results suggest that typically studied synesthetic sensory pairings may be just the tip of the iceberg, with other unusual cross-modal interactions yet to be discovered.

Although our approach was limited by the inherent difficulty of quantifying a phenomenon that is, at its core, a subjective perceptual sensation, our findings provide strong evidence against alternative explanations. First, we induced an experimentally controlled set of expectations designed to counteract possible response biases. Nevertheless, a large majority of participants gave reports that deviated from these explicit expectations, which supports the conclusion that participants indeed reported genuine visual sensations. Second, many of our participants reported experiencing unmistakable and highly visible visual sensations that are hard to explain by expectation biases—this was especially true for individuals with synesthesia. Third, the strength of an individual's mental imagery did not predict the strength of the reported visual sensation, which rules out an alternative explanation that participants were simply reporting mental images of hand motion. In a similar vein, mental images cannot drive the smooth-pursuit system (Jordan, 1970), and, therefore, mental imagery cannot explain the results of Experiment 5. Finally, we found that subjective reports of kinesthesis-induced visual sensations predict smoothness of pursuit eye movements in total darkness. As simply knowing one's own hand location in space is insufficient to drive smooth pursuit eye movements (Dieter, Hu, Knill, & Tadin, 2011; Watanabe & Shimojo, 1997), the most parsimonious explanation of the findings from Experiment 5 is that the observed smooth pursuit eye movements were driven by genuine visual sensation of motions.

In summary, we found empirical evidence that kinesthesis can be solely sufficient to generate normally concomitant visual sensations. This finding was derived from a simple approach in which an action was performed without its typical visual consequences; this approach allowed us to isolate the action's effects on visual processing. Overall, our results are consistent with the predictive-coding framework (Blakemore et al., 1999; Flanagan & Wing, 1997; Wolpert et al., 1995) and show that the brain relies heavily on prior experience, to a point that people can sometimes perceive things in the complete absence of the primary sensory input that ordinarily triggers that perceptual experience. More broadly, this phenomenon is a striking example of the remarkable ability of the nervous system to exploit predictive associations (DiCarlo, Zoccolan, & Rust, 2012; Di Luca, Ernst, & Backus, 2010; Pavlov, 1927).

Author Contributions

R. Blake and D. Tadin developed the study concept. K. C. Dieter, B. Hu, D. C. Knill, R. Blake, and D. Tadin contributed to the study design. K. C. Dieter, B. Hu, R. Blake, and D. Tadin collected the data. K. C. Dieter, B. Hu, and D. Tadin analyzed the data. K. C. Dieter and D. Tadin drafted the manuscript. All authors edited the manuscript and approved the final version for submission.

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Declaration of Conflicting Interests

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Notes

1. Across experiments, 11 of the 129 participants (8.5%) were excluded for procedural errors, which typically occurred when a participant inadvertently felt the front of the blindfold after the cardboard had been removed. These participants are not included in the total *N*s reported for each experiment.

2. Unless noted, statistical analyses were nonparametric (Mann-Whitney test, Wilcoxon signed-ranks test, and Spearman rank-order correlation).

References

Bargary, G., & Mitchell, K. J. (2008). Synaesthesia and cortical connectivity. *Trends in Neurosciences*, *31*, 335–342. doi:10.1016/j.tins.2008.03.007

Barnett, K. J., Finucane, C., Asher, J. E., Bargary, G., Corvin, A. P., Newell, F. N., & Mitchell, K. J. (2008). Familial patterns and the origins of individual differences in synaesthesia. *Cognition*, *106*, 871–893. doi:10.1016/j.cognition.2007.05.003

Bays, P. M., & Wolpert, D. M. (2007). Predictive attenuation in the perception of touch. In P. Haggard, Y. Rosetti, & M. Kawato (Eds.), *Sensorimotor foundations of higher cognition: Attention and performance XXII* (pp. 339–358). New York, NY: Oxford University Press.

Berryhill, M. E., Chiu, T., & Hughes, H. C. (2006). Smooth pursuit of nonvisual motion. *Journal of Neurophysiology*, *96*, 461–464. doi:10.1152/jn.00152.2006

Blakemore, S. J., Frith, C. D., & Wolpert, D. M. (1999). Spatiotemporal prediction modulates the perception of self-produced stimuli. *Journal of Cognitive Neuroscience*, *11*, 551–559.

Bolognini, N., Senna, I., Maravita, A., Pascual-Leone, A., & Merabet, L. B. (2010). Auditory enhancement of visual phosphene perception: The effect of temporal and spatial factors and of stimulus intensity. *Neuroscience Letters*, *477*, 109–114. doi:10.1016/j.neulet.2010.04.044

Botvinick, M., & Cohen, J. (1998). Rubber hands "feel" touch that eyes see. *Nature*, *391*, 756.

Carlson, T. A., Alvarez, G., Wu, D. A., & Verstraten, F. A. J. (2010). Rapid assimilation of external objects into the body schema. *Psychological Science*, *21*, 1000–1005.

Christensen, A., Ilg, W., & Giese, M. A. (2011). Spatiotemporal tuning of the facilitation of biological motion perception by concurrent motor execution. *The Journal of Neuroscience*, *31*, 3493–3499. doi:10.1523/jneurosci.4277-10.2011

Cole, J. (1995). *Pride and a daily marathon*. Cambridge, MA: MIT Press.

Davies, P. (1973). Effects of movements upon the appearance and duration of a prolonged visual afterimage: 1. Changes arising from the movement of a portion of the body incorporated in the afterimaged scene. *Perception*, *2*, 147–153.

DiCarlo, J. J., Zoccolan, D., & Rust, N. C. (2012). How does the brain solve visual object recognition? *Neuron*, *73*, 415–434.

Dieter, K. C., Hu, B., Knill, D. C., & Tadin, D. (2011). Visual smooth pursuit of proprioceptive signals is enhanced by task-irrelevant dynamic noise. *Journal of Vision*, *11*(11), Article 786. Retrieved from www.journalofvision.org/content/11/11/786

Di Luca, M., Ernst, M. O., & Backus, B. T. (2010). Learning to use an invisible visual signal for perception. *Current Biology*, *20*, 1860–1863.

Eagleman, D. M., Kagan, A. D., Nelson, S. S., Sagaram, D., & Sarma, A. K. (2007). A standardized test battery for the study of synesthesia. *Journal of Neuroscience Methods*, *159*, 139–145. doi:10.1016/j.jneumeth.2006.07.012

Ehrsson, H. H. (2007). The experimental induction of out-of-body experiences. *Science*, *317*, 1048. doi:10.1126/science.1142175

Flanagan, J. R., & Wing, A. M. (1997). The role of internal models in motion planning and control: Evidence from grip force adjustments during movements of hand-held loads. *The Journal of Neuroscience*, *17*, 1519–1528.

Funk, M., Shiffrar, M., & Brugger, P. (2005). Hand movement observation by individuals born without hands: Phantom limb experience constrains visual limb perception. *Experimental Brain Research*, *164*, 341–346. doi:10.1007/s00221-005-2255-4

Glenny, G., & Heywood, S. (1979). Hans Gertz revisited: The different effects of invisibility and darkness on pursuit eye movements. *Perception*, *8*, 31–36.

Gori, M., Del Viva, M., Sandini, G., & Burr, D. C. (2008). Young children do not integrate visual and haptic form information. *Current Biology*, *18*, 694–698. doi:10.1016/j.cub.2008.04.036

Gregory, R. L. (1958). Eye movements and the stability of the visual world. *Nature*, *182*, 1214–1216.

Hänggi, J., Wotruba, D., & Jäncke, L. (2011). Globally altered structural brain network topology in grapheme-color synesthesia. *The Journal of Neuroscience*, *31*, 5816–5828. doi:10.1523/jneurosci.0964-10.2011

Hu, B., & Knill, D. C. (2010). Kinesthetic information disambiguates visual motion signals. *Current Biology*, *20*, R436–R437. doi:10.1016/j.cub.2010.03.053

Jordan, S. (1970). Ocular pursuit movement as a function of visual and proprioceptive stimulation. *Vision Research*, *10*, 775–780.

Kowler, E. (2011). Eye movements: The past 25 years. *Vision Research*, *51*, 1457–1483.

Lally, N., Frendo, B., & Diedrichsen, J. (2011). Sensory cancellation of self-movement facilitates visual motion detection. *Journal of Vision*, *11*(14), Article 5. Retrieved from http://www.journalofvision.org/content/11/14/5

Linn, M. C., & Petersen, A. C. (1985). Emergence and characterization of sex differences in spatial ability: A meta-analysis. *Child Development*, *56*, 1479–1498.

Marks, D. F. (1973). Visual mental imagery in the recall of pictures. *British Journal of Psychology*, *64*, 17–24.

Maruya, K., Yang, E., & Blake, R. (2007). Voluntary action influences visual competition. *Psychological Science*, *18*, 1090–1098. doi:10.1111/j.1467-9280.2007.02030.x

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia*, *9*, 97–113.

Pavlov, I. P. (1927). *Conditioned reflexes: An investigation of the physiological activity of the cerebral cortex* (G. V. Anrep, Trans.). London, England: Oxford University Press.

Ramachandran, V. S., & Rogers-Ramachandran, D. (1996). Synaesthesia in phantom limbs induced with mirrors. *Proceedings of the Royal Society B: Biological Sciences*, *263*, 377–386.

Ramos-Estebanez, C., Merabet, L. B., Machii, K., Fregni, F., Thut, G., Wagner, T. A., . . . Pascual-Leone, A. (2007). Visual phosphene perception modulated by subthreshold crossmodal sensory stimulation. *The Journal of Neuroscience*, *27*, 4178–4181. doi:10.1523/jneurosci.5468-06.2007

Robertson, L. C., & Sagiv, N. (Eds.). (2005). *Synesthesia: Perspectives from cognitive neuroscience*. New York, NY: Oxford University Press.

Romei, V., Murray, M. M., Cappe, C., & Thut, G. (2009). Preperceptual and stimulus-selective enhancement of low-level human visual cortex excitability by sounds. *Current Biology*, *19*, 1799–1805.

Rouw, R., & Scholte, H. S. (2007). Increased structural connectivity in grapheme-color synesthesia. *Nature Neuroscience*, *10*, 792–797. doi:10.1038/nn1906

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), Article 2. Retrieved from www.journalofvision.org/content/13/7/2

Terhune, D. B., Tai, S., Cowey, A., Popescu, T., & Cohen Kadosh, R. (2011). Enhanced cortical excitability in grapheme-color synesthesia and its modulation. *Current Biology*, *21*, 2006–2009. doi:10.1016/j.cub.2011.10.032

Watanabe, K., & Shimojo, S. (1997). Suppressive effect of multimodal surface representation on ocular smooth pursuit of invisible hand. *Perception*, *26*, 277–285.

Wolpert, D. M., Ghahramani, Z., & Jordan, M. I. (1995). An internal model for sensorimotor integration. *Science*, *269*, 1880–1882.