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Kinesthesia can make an invisible hand visible

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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 if our own 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 individuals with synesthesia experience substantially stronger kinesthesia-induced visual sensations. Finally, we found that the perceived vividness of kinesthesia-induced visual sensations predicted participants' ability to smoothly eye-track self-generated hand movements in darkness, indicating that these sensations function like typical retinally-driven visual sensations. Evidently, even in the complete absence of external visual input, our brains predict visual consequences of our actions.

Keywords

Multisensory perception; visual motion perception; kinesthesia; synesthesia; predictive coding

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 our actions enable improved estimation of body states (Wolpert, Ghahramani, & Jordan, 1995) and compensation of pervasive sensory delays,

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allowing predictive control of dynamic motor behaviors (Flanagan & Wing, 1997). The efference signals can also alter perception—self-generated tactile stimuli like a “tickle” are felt less strongly than equivalent externally generated signals (Blakemore, Frith, & Wolpert, 1999).

Our 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 kinesthesia is critical to how we perceive our 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 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. 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 which conditions, naïve participants report experiencing kinesthesia-induced visual sensations. To provide an objective measure of these sensations, we 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

129 naïve participants (46 male) took part in this study. Unless noted, each individual participated in only one experiment. All procedures were approved by the institutional review board. Unless noted, statistical analyses were non-parametric (Mann-Whitney test, Wilcoxon signed-ranks test and Spearman rank-order correlation).

Experiment 1: self-motion

49 participants (17 male) completed this experiment. Our results revealed a tendency for males to show stronger results ($P=0.015$), paralleling previous findings of gender differences

in visual-haptic tasks (Linn & Petersen, 1985). We controlled for the mismatch in sample sizes across genders in the following way: For illustrations, frequency histograms were computed separately for the two genders and then averaged, i.e., we weighted male and female results equally. For relevant non-parametric analyses, we created a representative sub-sample of 17 female individuals whose frequency histogram best matched the full female sample (means within 1.4%; identical medians, min, max, and Q1; Q3 was 0.25 smaller in new sample) and combined these individuals with male participants, yielding N=34. All other experiments with typical individuals were balanced for gender.

During experimental trials, participants wore tightly fitting blindfolds (www.mindfold.com) 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 and experiments, 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, while the other had several dozen small hole-like indentations. Although both blindfolds blocked all light, participants were told that one blindfold would block “all light,” while 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 *maybe* to see something while wearing the other (Table 1).

All blindfold experiments (Experiments 1–4) consisted of two trials. On each trial in Experiment 1, 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. Crucially, participants were not told which blindfold was worn on which trial. Therefore on trial one, participants should consider it possible, though not necessarily likely, that they might have a visual experience. Expectations on trial two would depend on visual sensations experienced on trial one (Table 1). Specifically, seeing something on trial one creates an expectation of seeing nothing on trial two (but not necessarily vice versa if no visual sensation is experienced on trial one). Based on participant debriefing, we found that this approach was conservative in assessing the incidence and the strength of kinesthesia-induced visual sensations.

Procedure—To conceal the fact that hole-like indentations did not break the surface of the blindfold and to prevent participants from feeling the indentations, both blindfolds had cardboard stickers on the front. The two blindfolds were shuffled in front of each participant whose eyes were closed. The participant then selected one of the blindfolds and put it on. Once the blindfold was secure, the experimenter removed the stickers and asked the participant to open his/her eyes. This procedure was strictly followed. Across experiments, 11 participants (8.5%) were excluded for procedural errors, which typically occurred when a

participant inadvertently felt the front of the blindfold. Next, the experimenter verbally administered the Edinburgh Handedness Inventory (Oldfield, 1971). Participants were randomly assigned to use either their dominant or non-dominant hand in the experiment. We found no effect of hand dominance ($P=0.92$), so these data were combined.

Once a participant indicated 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/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. ...you had a visual sensation of motion?
3. ...you had a visual sensation of motion with direction?
4. ...the motion that you saw had any discernable shape or form?
5. ...the visual shape was vertically elongated, taller than it is wide?
6. ...the visual shape looked like the outline of a moving hand?

Participants were given a score (0–6) corresponding to the last question receiving a “yes” response. Participants sometimes expressed uncertainty at answering. In these cases, the experimenter disinterestedly reminded the participant that he/she must make a yes/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 study.

Experiment 2: self-motion, blindfold selection with replacement

20 participants (10 male) 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

16 participants (8 male) 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 used verbal cues to provide participants information about stimulus timing that was present in other experiments. Other details were as in Experiment 1.

Experiment 4: self-motion, participants with synesthesia

This experiment was identical to Experiment 1, except that participants ($N=9$, 1 male) were grapheme-color synesthetes. All synesthetes 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 experiencing both. No synesthete reported visuo-proprioceptive synesthesia.

Experiment 5: eye-tracking

20 non-synesthetes (10 male) and 6 synesthetes (0 male) participated. 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 (fixating and tracking). These six conditions were counterbalanced, each consisting of 3 trials (see below). Self- and experimenter-motion conditions were as described above. In the silhouette-motion condition, participants waved a cardboard silhouette of an arm (46 cm long) such that the hand portion (21 cm) passed in front of their eyes. In fixation conditions, participants were told to look straight ahead. In pursuit conditions, participants were instructed to follow the movement of the hand with their eyes. Following the explanation of these conditions, participants practiced (3 trials) visually pursuing their own hand in a lit room. Next, participants were familiarized with the rating statements (shown below) with which participants rated their disagreement/agreement on a 7-point Likert scale. Both statements of experimental interest and control statements (e.g., seeing other objects in the room) were included.

During the experiment there were times when I...

- ...had a visual sensation
- ...had a visual sensation of motion
- ...had a visual sensation of color
- ...had a visual sensation of a moving form
- ...had a visual sensation of the outline of a hand
- ...visually perceived individual fingers
- ...visually perceived other objects in the room

Eye position was tracked using a head-mounted eye-tracker (EyeLink II, SR Research). To ensure complete darkness, 900/925 nm illuminators were fitted with high-pass infrared filters whose efficacy was confirmed by dark-adapted observers. Eye tracking analysis was based on data from 20/26 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. 30 s later, a computer voice informed the participant (or the experimenter) to initiate hand waving. Each trial lasted 10 s. There were a total of 3 such trials, separated by 5 s breaks.

Eye position (sampled at 250Hz) was first smoothed with a 75-ms median filter and then with a 75-ms, 3rd order Savitzky–Golay filter, smoothing high-frequency variations without

flattening eye position). These position traces were differentiated to yield eye velocity. Saccades were defined by polar eye velocity that was 20°/s 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 ranges from 0, indicating only saccadic eye movements, to 1, indicating that only pursuit eye movements occurred.

Results

Experiment 1: self-motion

Participants wore blindfolds that blocked *all light* and made visual judgments while waving their hand in front of their blindfold-covered eyes (Fig. 1a). Under these conditions, ensuing visual experiences would be inherently subjective and possibly affected by response biases. To minimize such biases, participants received deceptive instructions designed to introduce experimentally controlled expectations (Table 1).

A majority of participants reported experiencing visual sensations while waving their hand (Fig. 1b). On trial one, ~50% of participants reported visual sensations, most commonly a “visual sensation of motion,” described during debriefing as a moving shadow or darkening. On trial two, participants who reported visual sensations on trial one would be explicitly biased against a second positive report (Table 1). Although this explicit bias to report no visual sensation did result in weaker overall ratings on trial two (Fig. 1b; $z=2.26$, $P=0.02$), 44% of those who reported visual sensations on trial one also reported visual sensations on trial two. Moreover, all but one individual who reported visual sensations on trial two had reported sensations on trial one—an observation that is unequivocally inconsistent with our deceptive instructions, but is consistent with the perceptual reality of the reported sensations. Notably, these ratings did not correlate with participants’ visual imagery ability ($r_s=-0.07$, -0.02 for trial one and two, respectively; all $P>0.67$), arguing against a significant role of visual imagery in the observed results.

Experiment 2: blindfold selection with replacement

This was a repetition of Experiment 1 with one change: now the two blindfolds were sampled with replacement. Participants were aware that they might select the same blindfold two trials in a row, effectively eliminating differences in expectations on the two trials. Indeed the incidence of seeing motion did not differ between the two trials in this experiment ($z=0.32$, $P=0.75$). Importantly, ratings did not differ from trial one ratings in Experiment 1 ($z=-0.92$, $P=0.37$).

Experiment 3: experimenter-motion

Here, the experimenter – not the participant – waved his hand in front of the blindfold, with all other details unchanged. Under these conditions, no participant reported visual sensations on trial one (Fig. 1c). These ratings were significantly weaker than both trial one and two ratings in Experiment 1 ($z=3.22$, 2.07 ; $P=0.001$, 0.038 , respectively) and significantly weaker than Experiment 2 ratings ($z=2.33$, $P=0.020$). Moreover, only 2/16 participants gave

positive reports on trial two (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

What causes the visual sensations experienced during self-generated hand movement? The perceptual reality of these reported sensations presumably requires functional connectivity between kinesthetic/proprioceptive areas and brain areas capable of generating visual sensations. Additionally, it is likely that the strength of such crossmodally-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 enhanced cortical connectivity and excitability would experience stronger kinesthesia-induced visual sensations. To pursue this possibility, we tested individuals with grapheme-color synesthesia, a condition defined by strong associations between sensory modalities and/or sub-modalities. While 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 higher cortical excitability (Terhune, Tai, Cowey, Popescu, & 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.

Repeating Experiment 1 with grapheme-color synesthetes, we found substantially stronger reports of visual sensations (Fig.1d). On trial one, all synesthetes reported experiencing visual perceptions, and these were considerably stronger than those of non-synesthetes ($z=4.38$, $P=10^{-5}$). Nearly all synesthetes reported perceiving visual form in addition to visual motion. Additionally, trial two ratings for synesthetes did not differ from those on trial one (Fig.1d, $P=0.25$), even though these individuals were led to expect to see *nothing* on at least one of the two trials (Table 1). During debriefing, synesthetes typically described their visual experiences as resembling an inverted pendulum or a well-defined moving dark bar. Synesthetic participants did not differ from typical participants in their ability to generate visual imagery ($z=-0.76$, $P=0.45$). 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

Finally, we asked whether kinesthesia-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 importantly dependent on visual motion signals (Kowler, 2011). While 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). Notably, previous investigations reported considerable individual variability in participants' visual pursuit of self-generated movements in total darkness (Glenny & Heywood, 1979; Jordan, 1970; Watanabe & Shimojo, 1997). We hypothesize 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 kinesthesia-induced visual sensations would exhibit smoother eye tracking of their hand motion in complete darkness. The assumption is that illusory visual sensations of hand motion would provide a “lock” for smooth pursuit eye movements, essentially functioning as retinally-driven motion sensations.

In this final experiment, participants performed three types of ‘hand’ motion: (a) self-motion (b) silhouette-motion and (c) experimenter-motion (Method). These conditions were performed, in separate blocks, while participants either fixated straight ahead or while they tried to visually pursue the moving hand. First, to assess the vividness of experienced visual sensations, Likert scale ratings were obtained (Fig. 2). A 3-way ANOVA revealed main effects of motion type and rating question ($F_{2,50}=19.6$, $F_{6,150}=49.5$, both $P<10^{-6}$). We also found an interaction between motion type and rating question ($F_{12,300}=4.8$, $P<10^{-6}$), which was largely driven by stronger visual motion and form sensations when participants performed self-generated movements (Fig. 2). Ratings were marginally higher in the fixation condition ($F_{1,25}=3.6$, $P=0.069$). 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. In particular, higher ratings for the visual sensation, motion, and moving form questions in the fixation condition drove an interaction between rating question and eye movement condition ($F_{6,150}=3.5$, $P=0.003$). Relatively similar ratings for the self-motion and silhouette-motion conditions suggest that the experienced sensations may also extend to hand-held objects (Carlson, Alvarez, Wu, & Verstraten, 2010). As in the previous experiment, there was a tendency for synesthetes to report stronger ratings, but this effect was much weaker (a median increase of one response on the Likert scale)—a result likely reflecting greater heterogeneity of synesthesia types in this experiment (Method). Importantly for our purposes, we observed considerable individual differences in reported 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 (Method). 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 (Fig. 3a). Confirming our hypothesis, pursuit component gain was predicted by visual sensation ratings. Specifically, individuals who described experiencing visual sensations of form and motion tended to make significantly smoother eye movements in darkness (Fig.3b). Similar results were found when we excluded participants with synesthesia (all $P<0.02$). Fig.4a shows eye traces whose pursuit component gains best match the data in Fig.3b. Evidently, affirmative visual sensation ratings are associated with noticeably smoother pursuit eye movements. As an extreme example, Fig.4b shows data for a synesthetic participant who reported vivid kinesthesia-induced visual sensations and exhibited nearly perfect smooth pursuit in total darkness.

Supporting results shown in Fig. 4b, we found significant correlations between pursuit component gain during self-motion and vividness ratings of accompanying visual sensation, visual motion, moving form and hand outline ($r_s=0.60, 0.59, 0.50, 0.46$, respectively; all $P<0.04$). Other ratings were uncorrelated with pursuit component gain (all $P>0.11$). In the silhouette-motion condition, we found trends between pursuit component gain and ratings of visual sensation and visual motion ($r_s=0.42, 0.43, P=0.065, 0.058$). No correlations were found in the experimenter-motion condition (all $P>0.14$).

Discussion

Our findings indicate that action-vision interactions go beyond cross-sensory modulations—kinesthesia 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, 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 distinguish between these two possibilities. While the efference copy has long been associated with predictive coding, there are also numerous reports of interactions between proprioception and vision (Introduction).

While 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, while others described seeing well-defined visual forms. Within this latter group were individuals with synesthesia, suggesting that sensory interconnectivity (Hänggi, et al., 2011; Rouw & Scholte, 2007) and/or cortical excitability (Terhune, Tai, Cowey, Popescu, & Cohen Kadosh, 2011) might play a role in kinesthesia-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 kinesthesia 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). While 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.

While our approach is 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 (Table 1). Nevertheless, a large majority of participants gave reports that deviated from these explicit expectations (Results), supporting

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, ruling 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), indicating that mental imagery cannot explain Experiment 5 results. Fourth and finally, we found that subjective reports of kinesthesia-induced visual sensations predict smoothness of pursuit eye movements in total darkness (Figures 3 & 4). 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 Experiment 5 findings is that the observed smooth pursuit eye movements are driven by genuine visual sensation of motions.

In summary, we report empirical evidence that kinesthesia can be solely sufficient to generate normally concomitant visual sensations. This finding was derived from a simple approach where an action is performed without its typical visual consequences, allowing us to isolate its 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 our brains rely heavily on prior experience, to a point that we 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 our nervous system to exploit predictive associations (Di Luca, Ernst, & Backus, 2010; DiCarlo, Zoccolan, & Rust, 2012; Pavlov, 1927).

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Fig. 1. Task illustration and results from the blindfold experiments

(a), Illustration of hand movements performed by participants in the self-motion experiment. Participants waved their hand back and forth in front of the blindfold and rated accompanying visual perceptions, if any. (b–d), Histograms showing perceptual rating distributions for Experiments 1, 3 and 4. Abscissa shows the rating scale described in Method. For all plots, dark bars show trial 1 ratings, while light bars indicate ratings on trial 2. Results show that typical observers can experience visual sensations when waving their own hand in total darkness, sensations that were considerably stronger in synesthetes.

Fig. 2. Visual perception ratings in the eye tracking experiment

Data for self-, silhouette-, and experimenter-motion conditions, showing median responses to each of 7 rating items (see Method). Solid shapes and horizontal bars show responses under fixation and pursuit instructions, respectively. Vertical lines indicate the interquartile range for the fixation data. Dashed horizontal lines indicate the neutral response ('neither agree nor disagree'). Results demonstrate that participants reported experiencing visual sensations of motion and form, but only when moving their own hand or a cardboard silhouette.

Fig. 3. Smoothness of eye movement in darkness

(a), Smoothness of eye movements, as estimated by pursuit component gain, in three motion conditions. Participants were able to execute smoother eye movements when tracking own hand movements (Tukey HSD Test). (b), A link between pursuit smoothness and reported visual sensations in the self-motion condition. For each rating question with more than 3 affirmative answers, participants were split into those reporting visual sensations (dark bars) and those responding negatively (light bars)—i.e., ‘agree’ vs. ‘disagree’ responses. The results show higher pursuit component gains for individuals responding affirmatively to experiencing visual sensations, motion and form (paired t-tests). The same was found for an aggregate response to those questions, constituting an index of hand “visibility” (far right bars). */**/* indicate $P < 0.05$, 0.01, 0.001, respectively. Error bars are SEM.

Fig. 4. Representative horizontal eye position traces from the self-motion condition in Experiment 5

(a), Two individual trials that best matched pursuit component gains shown in Fig. 3b, far right. Eye positions that comprised saccades are shown in bold. Conversely, thin lines indicate smooth pursuit eye movements. The top trace illustrates 20% pursuit component gain, which corresponds to the average pursuit gain for participants that had median ratings in the “disagree” range for visual sensation, motion and moving form questions. 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. **(b)**, Horizontal eye position trace for a synesthetic participant who exhibited near perfect smooth pursuit of self-motion in total darkness.

Table 1
Experimentally induced expectations for Experiments 1, 3, and 4

Utilizing deceptive instructions, we presented an experimentally controlled set of expectations. Based on these instructions, participants were led to believe that it was possible, though not necessarily likely, that they might experience a visual sensation on Trial 1. As outlined in the table, expectations on Trial 2 depend on the visual experience in Trial 1.

	Had a visual sensation on Trial 1	Expected blindfold	Expected visual sensation
Trial 1	N/A	Both equally likely	Low chance of having a visual sensation
Trial 2	No	Probably the "leaky" blindfold	Maybe will have a visual sensation
	Yes	The unaltered blindfold	Will not have a visual sensation