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Report

Learning to Use an Invisible Visual Signal for Perception

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Summary

How does the brain construct a percept from sensory signals? One approach to this fundamental question is to investigate perceptual learning as induced by exposure to statistical regularities in sensory signals [1–7]. Recent studies showed that exposure to novel correlations between sensory signals can cause a signal to have new perceptual effects [2, 3]. In those studies, however, the signals were clearly visible. The automaticity of the learning was therefore difficult to determine. Here we investigate whether learning of this sort, which causes new effects on appearance, can be low level and automatic by employing a visual signal whose perceptual consequences were made invisible—a vertical disparity gradient masked by other depth cues. This approach excluded high-level influences such as attention or consciousness. Our stimulus for probing perceptual appearance was a rotating cylinder. During exposure, we introduced a new contingency between the invisible signal and the rotation direction of the cylinder. When subsequently presenting an ambiguously rotating version of the cylinder, we found that the invisible signal influenced the perceived rotation direction. This demonstrates that perception can rapidly undergo "structure learning" by automatically picking up novel contingencies between sensory signals, thus automatically recruiting signals for novel uses during the construction of a percept.

Results

To convincingly show that new perceptual meanings for sensory signals can be learned automatically, one needs an "invisible visual signal," that is, a signal that is sensed but that has no effect on visual appearance. The gradient of vertical binocular disparity, created by 2% vertical magnification of one eye's image (the eye of vertical magnification [EVM]), can be such a signal [8–10]. In several control experiments (see Supplemental Data and Figure S1 available online), we ensured that EVM could not be seen by the participants.

The stimulus we used was a horizontal cylinder rotating either front side up or front side down. In its basic form, the cylinder was defined by horizontal lines with fading edges (Figure 1A). The lines moved up and down on the screen, thereby creating the impression of a rotating cylinder with ambiguous rotation direction (Movie S1A), so participants perceived it rotating sometimes as front side up and sometimes as front side down [11] (see also Supplemental Data).

We tested whether the signal created by 2% vertical magnification could be recruited to control the perceived rotation direction of this ambiguously rotating cylinder. To do so, we exposed participants to a new contingency. We used a disambiguated version of the cylinder that contained additional depth cues: dots provided horizontal disparity, and a rectangle occluded part of the farther surface of the cylinder (Figure 1B). These cues disambiguated the perceived rotation direction of the cylinder (see Figure S2A). In training trials, we exposed participants to cylinder stimuli in which EVM and the unambiguously perceived rotation direction were contingent upon one another (Figure 2A; Movie S1B). To test whether EVM had an effect on the perceived rotation direction of the cylinder, we interleaved these training trials (Figure 2A) with probe trials that had ambiguous rotation direction (Figure 2B). If participants recruited EVM to the new use, then perceived rotation direction on probe trials would come to depend on EVM. If participants did not recruit EVM, then perceived rotation direction would be independent of EVM.

Importantly, after exposure to the new contingency, all participants saw a majority of probe trials consistent with the rotation direction contingent with EVM during exposure—that is, the learning effect was highly significant (see Supplemental Data). However, the effect of exposure did not result in a complete disambiguation, because cylinders in probe trials were still seen to be moving sometimes front side up and sometimes front side down. The proportion of responses consistent with the contingency gradually increased over the course of the experiment, as shown in Figure 3. The two-parameter exponential fit depicted in the figure is obtained with an asymptote of 0.67 and a time constant of 76 training trials (corresponding to 19 interleaved probe trials). These results show that EVM affected perceived rotation direction by disambiguating the probe trials when interleaved with training trials.

We also asked whether the recruitment was sufficiently long lasting to have an effect on perception after exposure was completed. For this, participants were provided with a set of final probe trials. The rightmost data point in Figure 3 shows that the effect was retained beyond exposure. In Figure S3, we analyze the increase of the effect of recruitment across different days, as well as the time course of the decay of recruitment.

Discussion

It has long been debated how the visual system learns which signals are informative about any given property of the environment [1]. How does it know that certain signals extracted from the retinal images—for example, binocular disparities, relative image sizes, and certain retinal image motions—can be trusted as signals to construct a depth percept? Recent work showed that signals can be recruited for new perceptual uses, but the recruited signal was always clearly visible to the subject during the experiments [2–4]. This posed the question of whether high-level processes such as consciousness,

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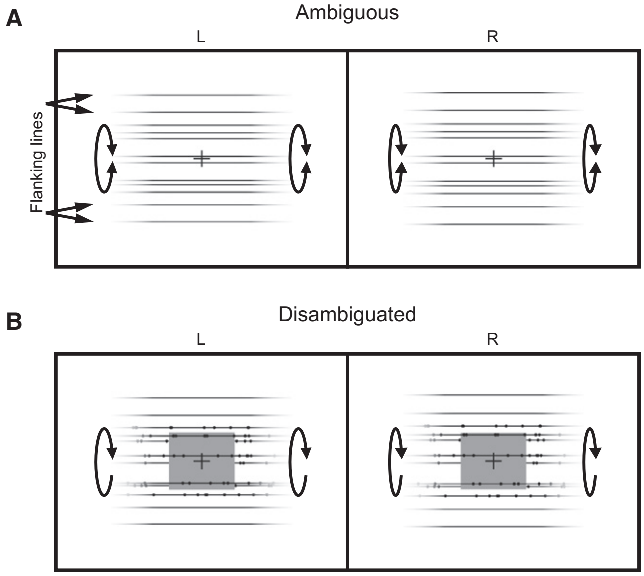

Figure 1. Stereoscopic Pair for Uncrossed Fusion

The right images are vertically magnified by 2% to create an invisible signal, eye of vertical magnification (EVM). See also Movies S1A and S1B.

(A) Cylinder with ambiguous direction of rotation (as indicated by the double arrow).

(B) Cylinder with added depth cues (horizontal disparity of dots and rectangle that occludes part of the back surface of the cylinder) that disambiguated rotation direction (indicated by the arrow).

awareness, attention, cognition, and any form of reward or incentives were necessary for learning new statistical regularities in general and for cue recruitment in particular.

We have demonstrated that exposure to a new contingency between an invisible signal (EVM) and an established percept (rotation direction of a cylinder) can cause the perceptual system to learn a new use for the EVM signal (cue to rotation direction, which disambiguates an otherwise ambiguous cylinder). That is, the vertical disparity signal affected perceptual appearance by disambiguating perceived rotation direction. This result indicates that associative learning in perception is an automatic learning process, does not require reinforcement, and can proceed without high-level processes such as cognition and attention. The process can detect contingencies between signals prior to the signal's use for constructing appearance.

Knowledge about human perceptual learning has increased greatly in recent years [12]. However, most work on perceptual learning measured refinements in the visual system's use of signals that it already used to perform a perceptual task, not the learning of new contingencies. One type of refinement is improvement in the ability to make fine discriminations between similar stimuli [13–18]. It was even shown that such an improvement in discrimination can occur for signals that are unseen [13]. A second type of refinement is recalibration, which occurs during reaching or throwing when a person wears prism goggles (e.g., [19–21]). Differentiation and recalibration are examples of "parameter" learning: learning that occurs by adjusting the use of signals that are already known to be useful [6, 22, 23].

Here we asked a different question, namely how (automatically) the perceptual system learns to use a novel signal to construct perceptual appearance. This form of learning from contingency can be described as "structure" learning (i.e., learning about statistical structure), insofar as a signal goes from being treated as independent of a scene property to being treated as conditionally dependent (and therefore useful to estimate the scene property) [22, 23]. In the Bayesian framework, structure learning is typically modeled by adding (or removing) edges, and sometimes nodes, in a Bayes net representation of dependence, whereas parameter learning requires no such changes to the graph structure of the Bayes net. Formally, however, structure learning can be implemented as an increase in the strength of a preexisting parameter that previously specified no conditional dependence [23]. Thus, starting to use a signal in a new way has sometimes been treated as parameter learning (e.g., [6]). However, dependency is qualitatively different from the absence of dependency; thus, consistent with usage elsewhere, we describe the acquisition of new knowledge about dependency to be structure learning [23]. Structure learning is generally considered to be more difficult than parameter learning [6].

Our results suggest that the goal of perceptual learning is to exploit signals that are informative about some aspect of the visual environment. The visual system cannot directly ascertain which signals are related to a property of the world. The only plausible way for it to assess whether a signal should be recruited is to observe how the signal covaries with already-trusted sources of information and their perceptual consequences. In principle, then, signals can sometimes be recruited to affect the appearance of world properties with which they are not normally linked [2, 24]. However, because two or more signals in ecological situations are usually correlated with each other only when they carry information about the same property of the environment [7, 25], the accidental recruitment of signals that are not valid is unlikely.

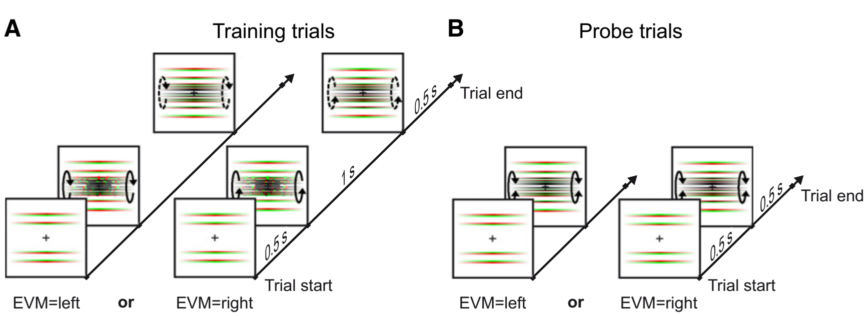

Figure 2. Timeline of Trials

Green and red show the images seen by the left and right eyes, respectively. All stimuli contained a rotating cylinder composed of lines and EVM.

(A) During training trials, the cylinder was first presented with depth cues that disambiguated rotation direction. Then the depth cues were removed, but perceived rotation direction was generally determined by the cues present at the beginning of the trials (see Figure S2A). The specified rotation direction was contingent on EVM (see Movie S1A).

(B) During probe trials, the cylinder was shown without disambiguating depth cues (see Movie S1B). If EVM is recruited, perceived rotation will be the same as the rotation associated with EVM during exposure.

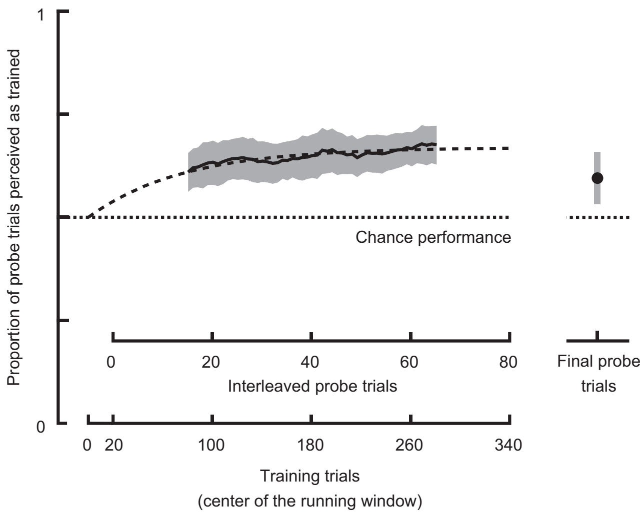

Figure 3. Proportion of Probe Trials Perceived Consistent with the Contingency during Exposure, Indicating Recruitment of EVM

Data for probe trials interleaved with training trials are shown. We used a running window of 30 probe trials to filter the data. Error bars represent 95% confidence intervals across participants calculated separately for each data point of the running average (see Supplemental Experimental Procedures). See also Figure S2 for further data analysis and Figure S3 for an additional experiment that investigates the buildup of learning over multiple days and the decay of the effect in the final probe trials.

Thus, these results suggest that humans possess a mechanism that automatically detects contingency between signals and exploits it to improve perceptual function and that has access to signals that need not have perceptual consequences (i.e., they can be unseen). Such a mechanism may, in fact, be necessary if the meanings of some cues must be learned by experience [1, 26, 27]. The newly recruited cue can then either stand in for a long-trusted cue when the latter is missing from a scene [3] or can be integrated with other cues to improve the accuracy and precision of perceptual estimates [28].

Experimental Procedures

Twenty naive volunteers (19–26 years old) took part after giving informed consent. They were recruited from the Subject Database of the Max Planck Institute, Tübingen. In return for their participation, they received payment of €8/hr. Participants had normal or corrected-to-normal vision (Snellen equivalent of 20/25 or better) and normal stereopsis of 60 arcsec or better (Stereotest circles; Stereo Optical) and were tested for anomalous color vision. The experiments were approved by the Ethik-Kommission der Medizinischen Fakultät of the Universitätsklinikum Tübingen.

Stimuli were produced using Psychophysics Toolbox [29, 30] and were displayed on a cathode ray tube monitor at a distance of 60 cm. All displayed elements were rendered on a violet background in blue and red for the left and right eyes, respectively. Colors were matched so that with a pair of Berezin ProView anaglyph lenses (red on left eye), stimuli would appear black in one eye and near-perfectly blended with the background in the other eye [31]. All displayed elements were fully visible in the central part of the screen and were blended into the background by reducing their contrast toward the screen edges.

Trials started with a zero disparity fixation cross (1.9° visual angle) and four flanking horizontal lines above and below the cylinder's location (5.5° and 7.5° from fixation). The purpose of these lines was to make EVM easier for the visual system to measure, because the window of integration for vertical scale disparity is typically about 20° in diameter [32]. After 0.5 s, a horizontal cylinder appeared (8° diameter). The cylinder rotated (14.4°/s angular speed) around its axis of symmetry, which passed through fixation. The cylinder could be displayed in two configurations, ambiguous or disambiguated (Figure 1). Ambiguous configuration used eight horizontal lines that contained no discontinuities and were blended into the background at the sides. In this way, the lines could only weakly support horizontal disparity signals and could not specify the rotation direction of the cylinder—i.e., perceived direction was ambiguous. Disambiguated configuration used 80 dots (0.25° diameter) randomly positioned on the eight visible horizontal lines, each of which was placed randomly within an equal sector around the cylinder's circumference. A gray rectangle (12° × 3.5°) occluded the central portion of the farthest side of the cylinder. The horizontal disparity of the dots and the rectangle specified the rotation direction—i.e., the perceived direction was unambiguous (cf. Figure S2A).

In training trials, the cylinder was presented in the disambiguated configuration for 1.0 s, after which the additional depth cues were removed, leaving the ambiguous cylinder for 0.5 s (Figure 2A). In probe trials, the cylinder was presented in the ambiguous configuration for 0.5 s (Figure 2B). Participants were instructed to fixate the central cross and report the perceived rotation direction of the cylinder in the ambiguous configuration at the end of each trial by pressing one of two buttons. In training trials, the perceived rotation direction of the cylinder in the ambiguous configuration was primed by the cylinder in the disambiguated configuration (see Figure S2A for data showing the induction of perceived rotation direction).

In all trials, there was 2% vertical magnification of one eye's image (EVM). This caused a scaling of the image away from the center—i.e., displacement of image elements increased linearly with distance above and below the line of sight. In training trials, EVM was contingent with the direction of rotation. The contingency was balanced across participants (for half of the participants, EVM was the right eye when the cylinder rotated front side up). Both contingencies contributed to the overall effect, so data were combined (Figure S2B).

The experiment started with 20 training trials lasting twice as long as specified in Figure 2A. Subsequently, participants were presented with 80 blocks of five trials composed of four training trials and one probe trial in random order. Participants were required to take two 2 min breaks during exposure. At the end, participants were presented with 40 probe trials. For half of the participants, before the final probe trials, there was another 2 min break. Data from these trials did not differ for the two groups, so they were combined for analysis.

Supplemental Information

Supplemental Information includes Supplemental Data, Supplemental Experimental Procedures, three figures, and one movie and can be found with this article online at doi:10.1016/j.cub.2010.09.047.

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Supplemental Information

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Supplemental Data

Main Experiment

The proportion of responses in interleaved probe trials consistent with the exposed contingency was significantly above chance level across participants (single sample t-test on arcsine-transformed performance against chance, $t(19)=8.15$, $p<0.001$). This effect was significant for 15 out of the 20 individual participants (95% confidence intervals). The effect of training was also present in the final probe trials ($t(19)=3.12$, $p=0.005$). We also fitted a two-parameter regression line on each of the participants' responses in interleaved probe trials in order to test whether learning increased during the course of the experiment (Fig. 3). The lines obtained were positively sloped (single sample t-test on the slopes against 0: $t(19)=2.15$, $p=0.045$).

Participants were interviewed and debriefed after the experiment. When asked, no participant reported noticing any systematic consistency between the direction of rotation and any other stimulus feature, including EVM. Six of the 20 participants reported that the front of cylinders in the ambiguous configuration moved downwards more often than upwards, consistent with the fact that 16 out of 20 participants exhibited an overall bias in this direction during the experiment. Two participants reported that the cylinder more often rotated front upwards. The preference for seeing most ambiguous cylinders rotating in one direction or the other decreases the effect of training as measured by the difference in rotation direction due to the EVM. The effect of EVM on probe trials, however, was present over and above these perceptual preferences.

Invisibility Experiment

The EVM signal could have *failed* to be invisible for two reasons: (a) in the case of large magnifications, the two eyes' images might be too different to be combined in a single binocular view (diplopia) [8], and (b) the cylinder might appear slanted in depth, so that one side appears to be further than the other (the so-called "induced effect") [8,9,10]. At the viewing distance of 60 cm, a 2% magnification specifies a slant of approximately 12°, although perceptual effects are substantially smaller even when stimuli do not contain perspective cues [9,SR1]. However, the horizontal lines present in the stimuli used here provide a strong slant cue based on the zero gradient of orientation in the vertical direction. The lines also move vertically up and down on the screen and remain parallel, so the structure-from-motion signal also specifies that the cylinder is frontoparallel, thus diminishing the perceived slant. Finally, the effect of EVM on apparent slant would be lower for cylinders shown using only the lines (Fig. 1A) rather than adding dots that support horizontal disparities (Fig. 1B) because the primary perceptual effect of vertical magnification is to affect how horizontal disparity is interpreted as slant [8,9,10].

To make sure that EVM remained invisible even after the signal is sensed and registered by the central nervous system [SR2,SR3], we adopted two strategies. First, we limited the difference in vertical size of the eyes' images to 2% to prevent diplopia [8,SR4] (see below for choice of 2%). Second, to define the cylinder we used parallel horizontal lines with fading edges, which provided a strong perspective cue thereby masking the induced effect [SR5]. In this way, the apparent slant due to EVM should be masked by the other depth cues. Together, these two manipulations should be able to make the effects of EVM invisible.

To test whether these manipulations were effective and thus the EVM signal was invisible, we asked participants to perform an oddity task where on each trial we presented three successive stimuli containing a rotating cylinder as in the main experiment. One of the three stimuli had EVM opposite to the other two and participants were instructed to indicate which stimulus was the odd-man-out. If any effects of EVM were visible (induced slant, differences in the diplopic image, etc), performance in identifying the odd-man-out should be higher than chance (0.33). The cylinder was shown with additional depth cues that disambiguated rotation direction (as the initial part of training trials in the main experiment) because the induced effect on slant that can help participants to perform the identification should be larger due to the presence of image features that supported horizontal disparities. Note further that it would have been impossible to test whether EVM was invisible on the probe trials: when using cylinders in the ambiguous configuration we have no control over the perceived direction of rotation—an uncontrolled feature of the stimulus which may be used by the participants for solving the odd-men-out discrimination task.

To determine the magnitude of vertical magnification at which the effects of EVM were invisible we ran two conditions. In the first condition, we did not provide feedback about the correctness of the answer or instructions on how the stimuli were generated. Average results across participants indicate chance performance at the three levels of vertical magnification tested (Figure S1A). Figure S1B shows individual subject data indicating that performance was not different from chance for each participant at every level of magnification. Thus, in conditions similar to the training trials in the main experiment, none of the participants was able to see the EVM signal.

To make an even stronger test for the invisibility, in a second condition we gave detailed instruction on how the EVM signals were generated and we provided feedback after every trial. Results indicate that even under these conditions average performance is not different from chance at any of the three levels of magnification tested (Fig. S1A). Fig. S1C shows, however, that the effects of 2% magnification became visible to 1 of the 7 participants. Interestingly, this participant reported to have performed the task based on changes in colour appearance between the three anaglyph stimuli due to diplopia and not changes in slant from vertical disparities. As predicted, at 4% and 6% magnification, the effect of EVM for Masked cylinders became visible to more participants most probably due to diplopia. Given the increase in discrimination performance with higher vertical magnifications, in the main experiment we picked the smallest EVM magnitude tested, i.e. 2%.

Overall results from this experiment confirm that the effect of EVM is invisible for the stimuli used for exposure to the new contingency in the main experiment at 2% vertical magnification.

Slant Detection Experiment

To confirm that the reason for not seeing the EVM signal was masking by the lines, we performed a further control experiment in which we showed cylinders that had the EVM signal but that were composed only of dots. By removing the lines we removed the strong perspective cue that specified the absence of slant. We instructed participants to look for the cylinder made of dots that had different apparent slant in the odd-man-out task. Feedback was provided after each trial. With this stimulus and task, 4 of 7 participants were able to perform the task based on differences in slant (95% confidence intervals). Average performance at our chosen level of magnification (2%) is different from chance (two-tailed t-test on arcsine-transformed performance against chance, $t(6)=3.39$, $p=0.015$).

Repeated Exposure Experiment

To measure the effect over the course of different days and its dropoff after exposure, participants repeated the main experiment for five times on consecutive days, always with the same contingency between EVM and rotation direction. The data obtained are shown in Figure S3. The exponential function is fitted to the data from the probe trials that were interleaved with exposure. It has an asymptote of 0.62 (proportion of perceived rotations consistent with EVM exposure). The time constant is 48 train trials (12 probe trials). The exponential curve shows no appreciable difference from the one obtained in the main experiment (Fig. 3), suggesting that the learning does not accumulate across days.

After the exposure (training) on each day, we measured the decay of recruitment using 40 consecutive probe trials. The three-parameter exponential function fitted to these probe trials, averaged across the five sessions, has an initial amplitude of 0.65 and asymptote of 0.48 (i.e. close to the default value of 0.5). The time constant is 60 train trials (15 probe trials). Thus the learning for EVM decayed quite quickly after exposure.

At the end of the five days, participants performed an oddity task based on EVM equivalent to the invisibility experiment but with 2% vertical magnification (no feedback). The stimulus used for this test was the cylinder with the added depth cues to make rotation unambiguously the same on all three stimuli of the trial. Removing the disambiguation would make the stimuli equivalent to probe trials, causing EVM to become visible by virtue of its new effect on apparent rotation direction. Average percent correct across the 120 trials was not different from chance for each participant (95% confidence intervals). This indicates that the EVM signal per se was not visible even after the 5 days of exposure to the contingency. That is, it is an invisible signal that is recruited for a new perceptual use not only at the beginning of the experiment, but also at the end.

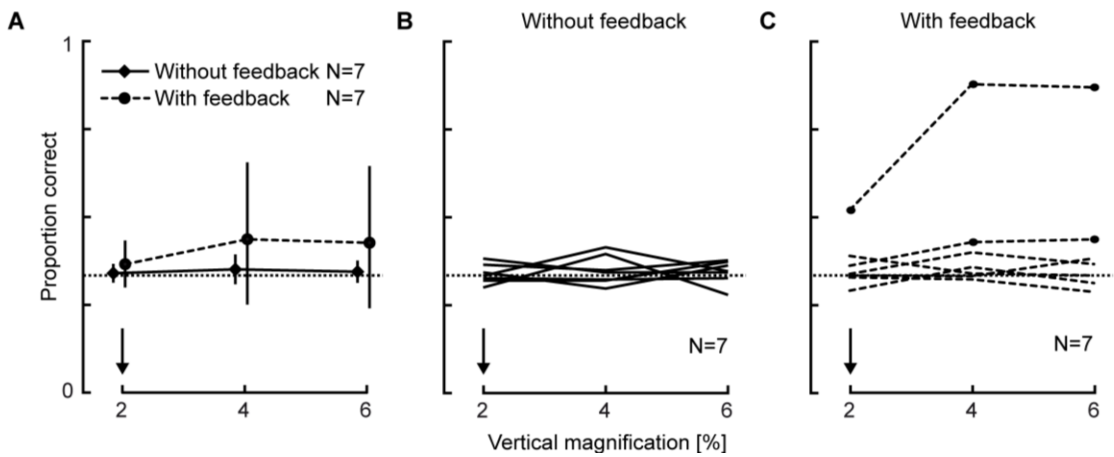

Figure S1. Proportion Correct Responses in an Odd-Man-Out Discrimination Task (One of Three Stimuli as Depicted in Figure 1B Having Different EVM from the Other Two) Plotted against the Magnitude of Vertical Magnification

Chance performance is 0.33 (dotted line). The arrows identify data for the vertical magnification used in the main and the repeated exposure experiments.

(A) Average performance in the discrimination of disambiguated cylinders based on EVM. Error bars represent 95% confidence intervals across participants (see Supplemental Experimental Procedures).

(B) Individual subject performance without feedback.

(C) Individual subject performance with feedback. Dots identify individual subject performance in the conditions where 95% confidence intervals based on the binomial distribution did not contain the chance value.

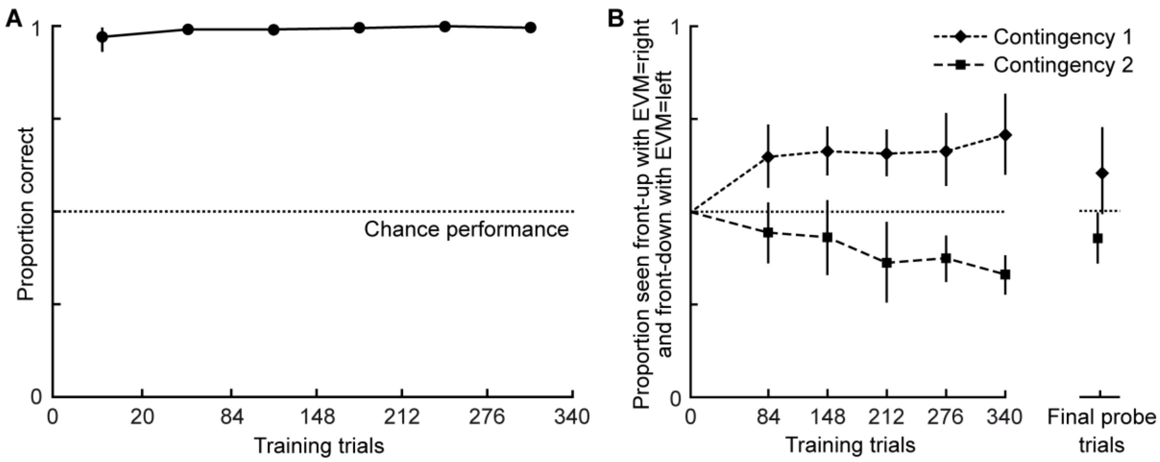

Figure S2. Additional Analyses of the Data in the Main Experiment
(A) Appearance of stimulus on training trials. On these trials the additional depth cues (horizontal disparity provided by dots, occluder) were present at the beginning of the trial (for 1.0 s) to prime the rotation of the cylinder, but not at the end (final 0.5 s). Data show that the depth cues were effective to disambiguate apparent rotation direction. Error bars represent 95% confidence intervals across participants (see Supplemental Experimental Procedures).
(B) Effect of EVM on probe trials for two groups of participants in the main experiment. The label on the ordinate reflects the fact that contingency was counterbalanced; participants in Group 1 were exposed to front-up cylinders paired with EVM=right (and front-down cylinders with EVM=left), while participants in Group 2 were exposed to front-up cylinders paired with EVM=left (and front-down cylinders with EVM=right). Error bars represent 95% confidence intervals across participants (see Supplemental Experimental Procedures).

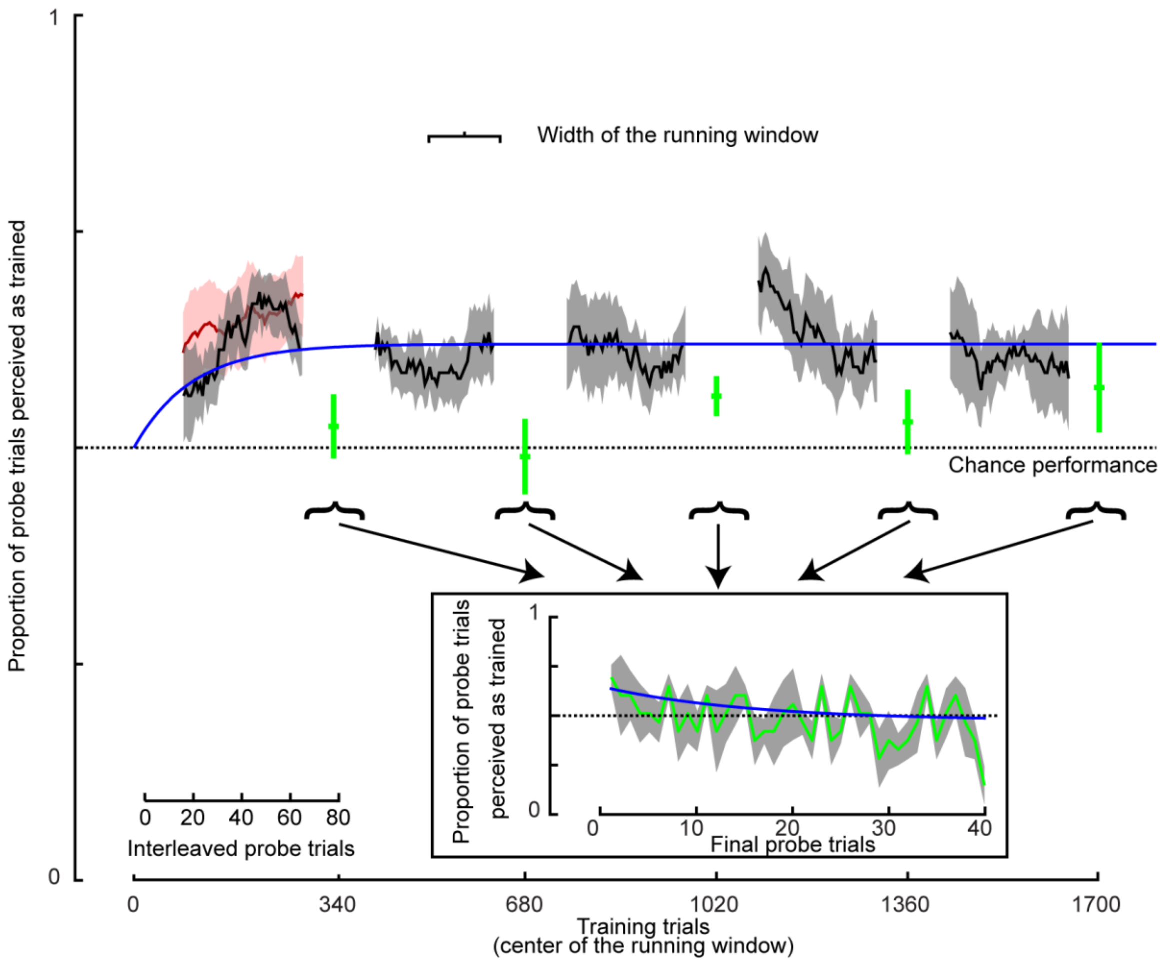

Figure S3. Result of Repeated Exposure in which the Main Experiment Was Repeated for Five Times on Five Consecutive Days

The data of 5 participants has been filtered using a running average with a width of 30 trials separately for each day. The black line indicates the running average across participants and grey areas indicate one standard error of the mean across participants. Green data points are the average of the 40 final probe trials. For ease of comparison, data indicated in red are replotted from the main experiment (Figure 3). The blue curve is an exponential function with two free parameters fitted to the data of the repeated exposure experiment (see Supplemental Data). The insert shows the data for the 40 final probe trials averaged across the five days and the 5 observers. The blue curve is an exponential function with three parameters fitted to the data.

Supplemental Experimental Procedures

Invisibility Experiment

Fourteen naïve volunteers (22-31 years) took part to the experiment to test that the EVM signal was not visible. Three cylinders were presented for 1s each, starting 0.5 s after the four flanking lines were made visible. Depth cues were added to the cylinder so to make them similar to the training trials in the main experiment. Participants were required to fixate the cross and report which of the three cylinders was different by pressing one of three buttons (3IFC oddity task). EVM was left (or right) in one of the three cylinders and right (or left) in the other two. Otherwise the stimuli in the three intervals were identical, all rotating in the same direction, randomized across trials. Each condition consisted of 360 trials, 120 for each image magnification: 2% (same magnitude as in the main experiment), 4%, and 6%. In the first condition 7 participants didn't receive particular instruction except that they had to find the odd-man-out. In the second condition the other 7 participants were told about EVM and its potential perceptual consequences and they received feedback on each of their responses ("correct" or "it was number 1/2/3" according to the EVM on that trial).

Slant Detection Experiment

Seven naïve volunteers took part. This experiment was equivalent to the invisibility experiment, except that the cylinder was displayed without the horizontal lines (leaving only the dots and the square). Participants were explicitly asked to compare the perceived slant of the cylinders and to report which of the three cylinders had a different orientation.

Calculation of Confidence Intervals

Confidence intervals were calculated on the average proportions of responses for each participant after transformation to standard scores using the inverse cumulative normal transformation (probit). The values obtained were then converted back to proportions of responses using the cumulative normal distribution function.

Supplemental References

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SR4. Duke, P.A., Oruc, I., Qi, H. and Backus, B.T. (2006). Depth aftereffects mediated by vertical disparities: calibration of extraretinal signals during stereopsis. Vision Research, 46, 228-241.
SR5. Saunders, J.A., and Backus, B.T. (2006). Perception of surface slant from oriented textures. Journal of Vision, 6, 882-897.

Supplemental Movie M1

Click here to download Supplemental Movie and Spreadsheet: Movie.m4v