Vision Research 178 (2021) 1–11

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Persistent grasping errors produce depth cue reweighting in perception

Evan Cesanek [a,1,*], Jordan A. Taylor [b], Fulvio Domini [a]

[a] Department of Cognitive, Linguistic, & Psychological Sciences, Brown University, Providence, RI, United States
[b] Department of Psychology, Princeton University, Princeton, NJ, United States

ARTICLE INFO

Keywords:
Sensorimotor adaptation
3D shape perception
Cue combination
Reach-to-grasp

ABSTRACT

When a grasped object is larger or smaller than expected, haptic feedback automatically recalibrates motor planning. Intriguingly, haptic feedback can also affect 3D shape perception through a process called depth cue reweighting. Although signatures of cue reweighting also appear in motor behavior, it is unclear whether this motor reweighting is the result of upstream perceptual reweighting, or a separate process. We propose that perceptual reweighting is directly related to motor control; in particular, that it is caused by persistent, systematic movement errors that cannot be resolved by motor recalibration alone. In Experiment 1, we inversely varied texture and stereo cues to create a set of depth-metamer objects: when texture specified a deep object, stereo specified a shallow object, and vice versa, such that all objects appeared equally deep. The stereo-texture pairings that produced this perceptual metamerism were determined for each participant in a matching task (Pre-test). Next, participants repeatedly grasped these depth metamers, receiving haptic feedback that was positively correlated with one cue and negatively correlated with the other, resulting in persistent movement errors. Finally, participants repeated the perceptual matching task (Post-test). In the condition where haptic feedback reinforced the texture cue, perceptual changes were correlated with changes in grasping performance across individuals, demonstrating a link between perceptual reweighting and improved motor control. Experiment 2 showed that cue reweighting does not occur when movement errors are rapidly corrected by standard motor adaptation. These findings suggest a mutual dependency between perception and action, with perception directly guiding action, and actions producing error signals that drive motor and perceptual learning.

1. Introduction

From one situation to the next, there are variations in the quality of the depth cues that create our visual perception of 3D shape. As a result, the visual system must adjust how it processes and combines depth cues in different viewing contexts to accurately perceive objects and plan object-directed actions. In some cases, the visual system can make immediate, stimulus-driven adjustments to its cue-combination function that are approximately optimal for the viewing context (Maloney & Landy, 1989; Young, Landy, & Maloney, 1993; Knill & Saunders, 2003; Hillis, Watt, Landy, & Banks, 2004; see also Ernst & Banks, 2002; Ghahramani, Wolpert, & Jordan, 1997). For example, the weight of texture information in determining perceived slant increases when viewing deeper slants, consistent with the stronger covariation between texture and physical shape at deeper slants. Similarly, the weight of stereo decreases with viewing distance, as binocular disparities diminish. In general, stereo is a more informative depth cue at viewing distances of a few meters (*i.e.*, within and just beyond arm's reach), while texture is the dominant cue for more distant viewing, such as an open landscape. However, in unfamiliar viewing contexts, the optimal way to combine cues may not be known ahead of time, leading to biased or noisy estimates of 3D shape (Johnston, 1991; Norman, Todd, Perotti, & Tittle, 1996; Norman, Lappin, & Norman, 2000; Domini & Caudek, 2003; Bingham, Crowell, & Todd, 2004). In this study, we investigated when and how sensory feedback from visually guided movements might be leveraged to gradually improve the accuracy of 3D shape perception.

Taking an ecological approach to this question, we begin by asking whether discrepancies between perceived and physical 3D shape actually pose a problem to the proper functioning of the agent. From the perspective of accurate motor behavior, it is not particularly problematic if suboptimal cue combination produces a constant bias in 3D shape perception. In this case, movement planning can rapidly compensate for the perceptual bias through sensorimotor adaptation (von Helmholtz, 1962; Held & Hein, 1958; Welch, 2013; Redding & Wallace, 1997;

---

* Corresponding author.
E-mail address: eac2257@columbia.edu (E. Cesanek).

[1] Present address: Zuckerman Mind Brain Behavior Institute, Department of Neuroscience, Columbia University, New York, NY.

https://doi.org/10.1016/j.visres.2020.09.007
Received 16 March 2020; Received in revised form 8 September 2020; Accepted 17 September 2020

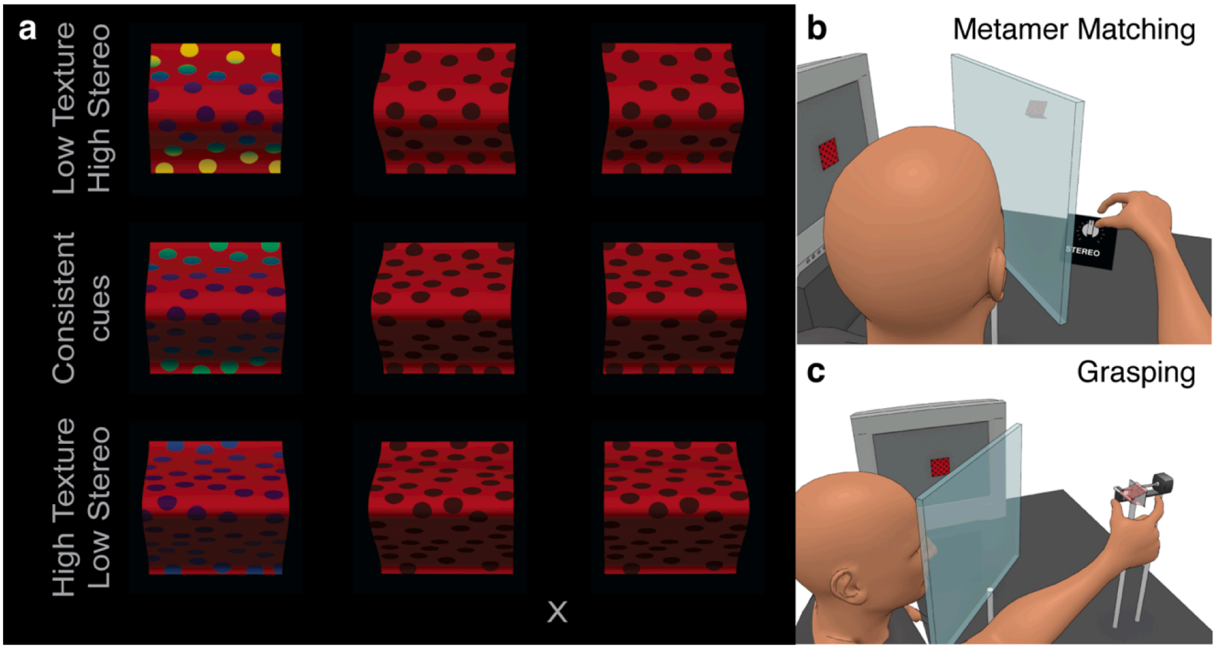

Fig. 1. Tasks and stimuli. (a) Example metamers (based on average Pre-test results): a 30-mm cue-consistent standard (middle) is perceived to have the same depth as the combination of 18 mm of texture depth with 37 mm of stereo depth (top), as well as the combination of 42 mm of texture depth with 23 mm of stereo depth (bottom). At left, cyclopean views with stereo depth coded by a color gradient. At right, corresponding stereograms (cross-fuse). (b) In the perceptual task (Pre-test and Post-test), participants created depth metamers by adjusting the *stereo* depth of a cue-conflict stimulus to match the perceived depth of the cue-consistent standard depicted in middle row of panel a. The adjustable cue-conflict had a fixed value of texture depth that differed from the standard. (c) The grasping task involved two different haptic feedback conditions, haptic-for-texture and haptic-for-stereo. Each participant completed both conditions, completing the entire experiment (Pre-test, Grasping, and Post-test) on two separate days. In the haptic-for-texture condition, haptic feedback reinforced the texture cue; in the haptic-for-stereo condition, haptic feedback reinforced the stereo cue. The design of the depth-metamer stimulus set ensured that when haptic feedback reinforced one cue, it was negatively correlated with the other cue.

Shadmehr, Smith, & Krakauer, 2010; Cesanek & Domini, 2017; Cesanek, Taylor, & Domini, 2020). Thus, no change in perceptual processing is needed, providing a simple explanation of the empirical reality that evidence of *bona fide* changes to visual perception in classic sensorimotor adaptation paradigms remains scant, despite over a century of investigation (Harris, 1965; Ostry & Gribble, 2016). In contrast, when a depth cue that is poorly correlated with physical shape is given too much influence in cue combination, *variable* errors will occur in 3D shape perception rather than constant biases. Variable perceptual errors pose a more nefarious problem for motor control, as sensorimotor adaptation is largely ineffective in resolving them. For instance, when reaching for an object whose depth is underestimated due to an unreliable depth cue, the fingers might contact the object sooner than expected. Grasp planning would then be recalibrated to produce a wider grip aperture in the future. However, the same unreliable cue might cause you to overestimate the depth of the next object you reach for, so the recalibrated grip aperture will not help; this time, your fingertips may completely miss the intended contact points. Over time, the conflicting recalibrations would simply oscillate, allowing the variable errors to persist. To perform accurately in this situation, the motor system must change how it relies on available depth cues.

One way to do this is by exploiting sensory feedback from object-directed movements as a teaching signal. Several previous studies have demonstrated that when haptic feedback from an object is consistent with one depth cue and inconsistent with another, perceptual cue reweighting occurs (Atkins, Fiser, & Jacobs, 2001; Ernst, Banks, & Bülthoff, 2000; Ho, Serwe, Trommershäuser, Maloney, & Landy, 2009). For single-cue stimuli, haptic feedback also can induce perceptual changes, although in this case the process is typically referred to as depth cue recalibration, not reweighting (Adams, Banks, & van Ee, 2001; Adams, Kerrigan, & Graf, 2010; Atkins, Jacobs, & Knill, 2003). Though little is known about the underlying learning mechanisms of either process, it is important to note that all previous studies on this topic have involved variable movement errors. Indeed, we recently confirmed experimentally that variable errors are necessary to drive cue reweighting, whereas fixed mismatches between perceived size and haptic feedback (*i.e.*, constant biases) are not sufficient (Cesanek & Domini, 2019). However, in that study, we measured the relative influences of depth cues based on a visuomotor response variable: the maximum grip apertures (MGA) of grasping movements. Likewise, other previous studies on visuomotor cue reweighting have focused on the grip orientation during interactions with slanted surfaces without studying changes in perceived slant (Cesanek, Taylor, & Domini, 2020; van Beers, van Mierlo, Smeets, & Brenner, 2011). Therefore, the existing findings leave open the possibility that there is a fundamental difference between vision-for-action and vision-for-perception, such that visuomotor cue reweighting might reflect a qualitatively different phenomenon than perceptual cue reweighting.

The aim of the current experiment was to demonstrate that cue reweighting in motor control is the result of upstream perceptual reweighting, and that perceptual reweighting is caused by persistent, systematic movement errors. Our hypothesis is that the perceived 3D shape of an object is used to guide visuomotor behaviors like grasping, and that the processes that combine depth cues for visual perception are sensitive to error signals received during these visuomotor behaviors. This hypothesis stands in contrast to the idea that visuomotor behavior is guided by separate, non-perceptual processing of depth cues, often called “vision-for-action”. To produce systematic movement errors, we had participants interact with *depth metamer* stimuli in our main experiment. Depth metamers are objects perceived to have the same depth, despite being composed of different combinations of the component depth cues. With two available cues, they can be created by inversely varying the cue values so that they perceptually negate one another (see examples in Fig. 1a).

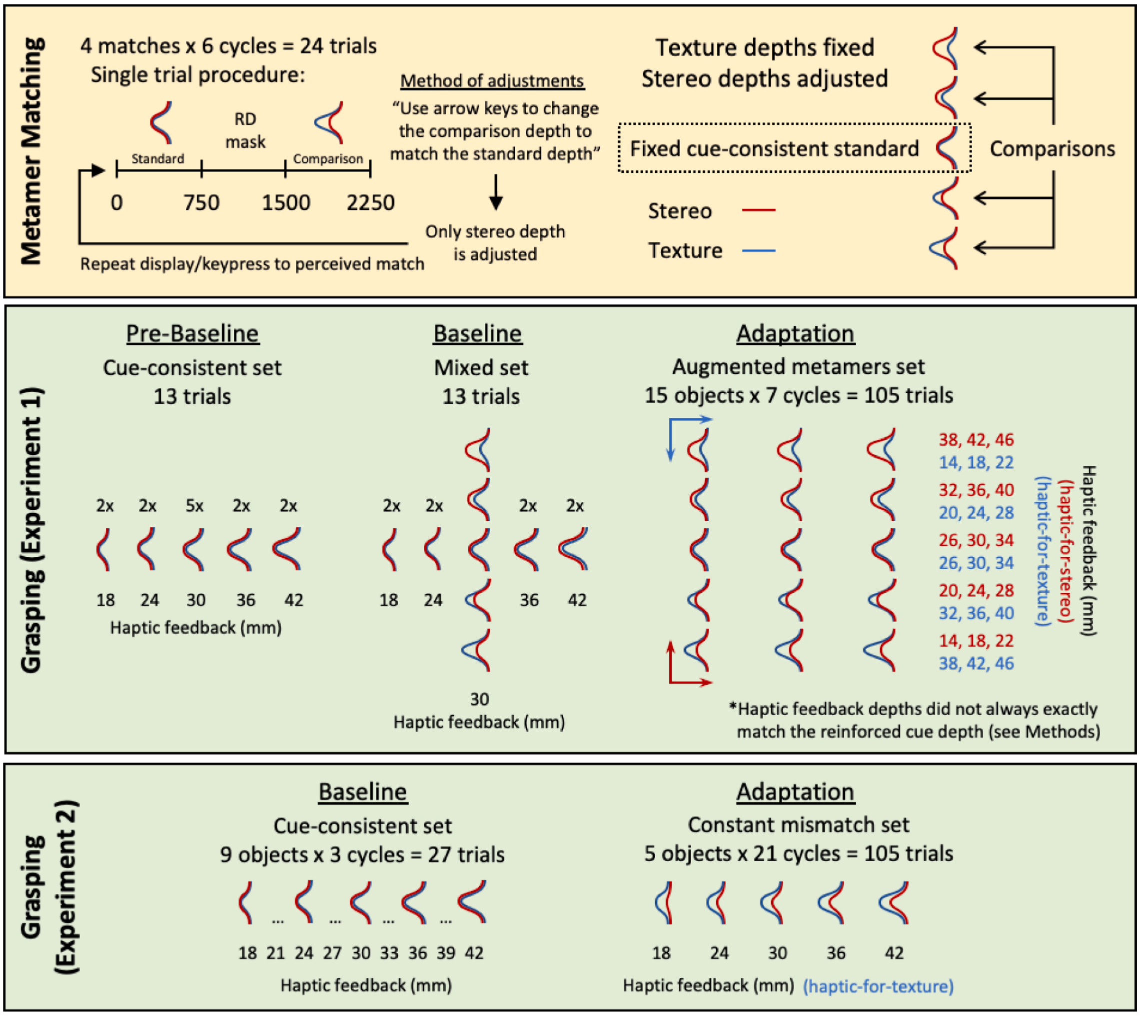

Fig. 2. Schematic of the stimulus sets and procedure for the Metamer Matching and Grasping tasks. Red and blue ridges depict the stereo and texture values of the stimuli. Metamer Matching: In the Pre-test and Post-test, participants created a set of 5 metamer stimuli. The metamers were adjusted to have the same perceived depth as a 30-mm cue-consistent standard stimulus. Each metamer had a fixed value of texture depth that differed from the standard, ranging from 18 to 42 mm. Participants adjusted the stereo depth of each comparison stimulus to compensate for the fixed difference in texture depth (but were not informed that they were only adjusting the stereo depth). Within a trial, the standard and comparison were displayed in sequence, separated by a random-dot mask (750 ms each). Keypresses changed the stereo value of the comparison and caused the two-interval sequence to be displayed again. Participants were asked to terminate each trial when the two stimuli appeared to have the same depth. Six matches were obtained for each of the four comparison stimuli. Grasping (Experiment 1): In the Pre-Baseline phase, participants grasped a set of cue-consistent objects with corresponding haptic feedback. In the Baseline phase, the 30-mm cue-consistent object was replaced by the set of 5 metamers indicated in the Pre-test metamer matching. In the Adaptation phase, we presented the augmented set of metamers formed by locally shifting the Pre-test matches to create some variability in perceived depth, with fixed haptic feedback determined by the condition (numbers at right). Note that the haptic feedback depths were fixed across all subjects, so they did not always match the value of the reinforced cue, which depended on the Pre-test matches generated by the subject. However, haptic feedback was always positively correlated with the reinforced cue. Grasping (Experiment 2): Nine cue-consistent stimuli were grasped in the Baseline phase. In the Adaptation phase, participants grasped five stimuli with a constant 10-mm offset between stereo and texture. Haptic feedback matched the texture depth. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

To create personalized depth metamers, each participant in our experiments paired five increasing values of texture depth with five decreasing values of stereo depth (metamer matching task; Fig. 1b). When the stereo-texture pairings are chosen according to the observer's personal cue-weighting function, the perceived depths will be identical despite differences in the component stereo and texture values. For example, if your perception relies equally on stereo and texture information, you would perceive as equally deep (1) a rendered object composed of a stereo depth of 25 mm and a texture depth of 35 mm and (2) an object composed of a 40-mm stereo depth and a 20-mm texture depth—both pairings combine to a perceived depth of 30 mm. This is unlike normal visual experience where the magnitudes of stereo and texture signals both tend to increase with the physical depth of objects. However, the introduction of mismatches *per se* is not unrealistic, as perceived shapes from different depth cues typically do not align (Domini & Caudek, 2010), similar to the persistent misalignment of vision and proprioception in hand localization (Smeets, van den Dobbelsteen, de Grave, van Beers, & Brenner, 2006). Conveniently, the depth metamers created by each participant allow us to estimate the relative weights of the two cues in perception. Note that when estimating cue weights, we make the simplifying assumption that texture depth is metrically estimated based on the assumption of a regular polka-dot pattern on the object surface.

Through visuomotor interactions with these metamer stimuli (grasping task; Fig. 1c), we provided haptic feedback about their physical shapes, aiming to change the relative weights of stereo and texture so participants would become sensitive to the physical depth variation across the stimulus set. To do this, we selectively reinforced one of the two cues with positively correlated haptic feedback. Given the design of the metamer set, when haptic feedback is positively correlated with one cue, it is negatively correlated with the other. Specifically, in our haptic-for-texture condition, physical depth increased with texture depth, while in our haptic-for-stereo condition, physical depth increased with stereo depth. Note that this arrangement causes participants to make variable movement errors: for some stimuli, the unreliable depth cue specifies a spuriously large depth, causing a too-large grip aperture, but for other stimuli, the unreliable cue specifies a spuriously small depth, causing a too-small grip aperture. Following the grasping task, participants again completed the metamer matching task described above, in a perceptual Post-test. Each participant was exposed to the haptic-for-texture and haptic-for-stereo conditions in separate sessions occurring on different days.

In summary, each session of Experiment 1 was composed of a perceptual Pre-test to identify a personalized set of metamers, a grasping task where haptic feedback reinforced one of the two depth cues in the metamer set, and a perceptual Post-test to measure for changes in cue weights from Pre-test. In Experiment 2, we used a different set of stimuli during the grasping task, introducing a constant bias in stereo while keeping haptic feedback consistent with texture, in order to show that cue reweighting is not obtained in the absence of persistent errors.

2. Methods

2.1. Participants

Fifty-six participants were recruited for Experiments 1 ($N = 36$) and 2 ($N = 20$). Participants were between 18 and 35 years old, right-handed, and had normal or corrected-to-normal vision. They were either granted course credit or paid $8/hour as compensation. Written, informed consent was obtained from all participants prior to any participation. Our protocol was approved by the Brown University Institutional Review Board and performed in accordance with the ethical standards set forth in the 1964 Declaration of Helsinki.

2.2. Apparatus

Participants were seated in a height-adjustable chair so that the chin rested comfortably on a chinrest. Right-hand movements were tracked using an Optotrak Certus. Small, lightweight posts containing three infrared emitting diodes were attached to the fingernails of the index finger and thumb, and the system was calibrated to track the tips of the distal phalanxes of each finger. This motion-capture system was coupled to a virtual reality environment consisting of a half-silvered mirror slanted at 45° that reflected the stereoscopic image displayed on a 19″ CRT monitor positioned at the correct distance to provide consistent accommodative and vergence information (Fig. 1).

Participants viewed stereoscopic renderings of 3D objects with stereo and texture information controlled independently via backprojection. The object shapes were based on a single cycle of a cosine function, where the top and bottom edges were the farthest points from the observer and the middle protruded toward the observer. The square bases diagonally subtended 8° of visual angle. Objects were centered at eye level and viewed from a distance of 40 cm. Stereoscopic presentation was achieved with a frame interlacing technique in conjunction with liquid–crystal goggles synchronized to the frame rate. Stereoscopic visual feedback of both the index finger and thumb, in the form of small dots, was provided until one of the two fingers came within 25 mm of the target object, to prevent online visual feedback from unintentionally reinforcing stereo.

Haptic feedback was provided by a custom-built apparatus that used a stepper motor to control the separation between a piece of curved plastic in front and a flat surface in rear (the tip and base of the object). Precise alignment between this physical object and the rendered 3D stimuli was established at the start of each session. Before every trial, this alignment was checked using Optotrak markers on the physical object and corrected if necessary. Participants were allowed to practice grasping the object while the room lights were still on, before the occluding panel was placed on the mirror, calibrating their reaches to its general position.

2.3. Procedure

Fig. 2 provides a schematic of the procedure for the Metamer Matching task (same procedure for Pre-test and Post-test), and the Grasping tasks in Experiment 1 and 2. On each trial of the Metamer Matching task, participants were repeatedly shown the 30-mm cue-consistent standard, followed by a 5-cm^3 random dot cloud (a mask that also served to prevent stereo fatigue effects), followed by the adjustable cue-conflict stimulus with their current stereo depth setting. Each stimulus was displayed for 750 ms. The adjustable cue-conflict had one of four fixed texture depths (18, 24, 36, or 42 mm) and participants used keypresses to incrementally change the stereo depth until they reported a perceptual match. Every keypress resulted in the two objects being displayed again in sequence, as described above. Participants performed six repetitions with each of the four cue-conflicts for a total of 24 trials. The Pre-test and Post-test phases were identical.

On each trial of the grasping task, participants reached toward the target and applied a front-to-back precision grip. Trials began with the fingers pinched closed at the top of a small metal rod located below and to the right of the object, and about halfway between the eyes and the object. Participants were required to view the object for 500 ms plus a random jitter of 0–100 ms before receiving the “go” signal. Participants then had 2 s to successfully complete the trial. To successfully complete a trial, participants were required to place the thumb on the plastic contact at the front tip of the object, the index finger on the rear of the object, and to hold still for 300 ms. If they did so within the allotted time, a pleasant feedback tone was played, otherwise an aversive buzzing noise was played.

In Experiment 1, Pre-Baseline phase of grasping consisted of 13 trials where participants grasped cue-consistent stimuli with depths of 18, 24, 30, 36, and 42 mm. The 30-mm stimulus was repeated five times while the others were repeated twice. Next, in the Baseline phase, which was also 13 trials, we retained the 18, 24, 36, and 42-mm cue-consistent stimuli, presenting them two more times each, but the 30-mm cue-consistent stimulus was replaced by the participant’s personalized set of five depth metamers. During these first five presentations of the metamers, the underlying haptic depth was always 30 mm. Next, in the Adaptation phase, we presented the depth metamers from Pre-test, paired with haptic depths of 18, 24, 30, 36, and 42 mm. In the haptic-for-texture condition, haptic depths matched the fixed texture depths, and were therefore negatively correlated with stereo depth. In the haptic-for-stereo condition, the same five haptic depths were matched up in the opposite order across the metamer set. As a result, haptic depths were positively correlated with stereo depths, but did not exactly match them, and were perfectly negatively correlated with texture depths. To provide some variation in perceived depth during the Adaptation phase of Experiment 1, we replicated the five metamers indicated in Pre-test, shifting the stereo and texture depths for each metamer by 2D vector distances of ± 4 mm, perpendicular to the best-fit line through their Pre-test data (see Fig. 2). The corresponding haptic feedback was also shifted by ± 4 mm. These fifteen objects were presented in seven bins, for a total of 105 Adaptation trials. In the haptic-for-texture condition, the Pearson correlation coefficient between haptic and texture depth was $+0.93$, and between haptic and stereo depth was -0.31. In the haptic-for-stereo condition, the correlation between haptic and texture depth was -0.76, and between haptic and stereo depth was $+0.87$. For more details on how the augmentation procedure gives rise to these correlations, see Appendix.

In Experiment 2, the Baseline phase involved nine cue-consistent stimuli (18–42 mm in 3-mm increments), presented over three bins for

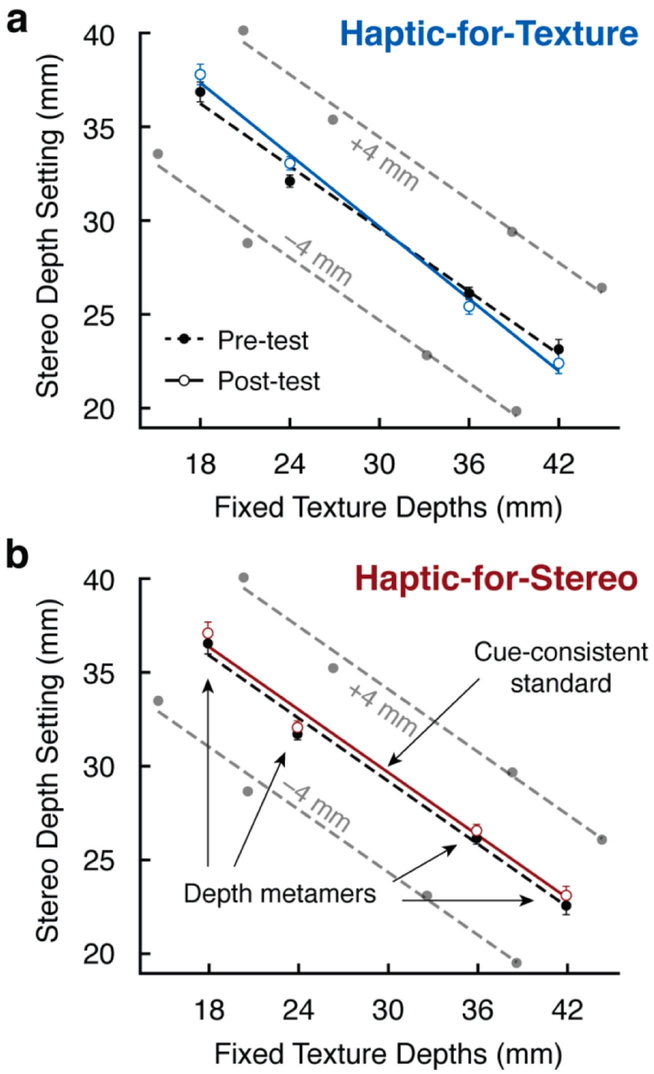

Fig. 3. Experiment 1 perceptual results. In the Pre-test and Post-test phases (see legend), participants created a personalized set of five depth metamers. The standard was a 30-mm cue-consistent stimulus (not plotted). For the other four stimuli, texture depths were fixed at 18, 24, 36, or 42 mm (x-axis) and the participant adjusted stereo depth (y-axis) until the perceived depth matched the standard. Gray points and dotted lines depict the additional stimuli presented in the Grasping task in order to provide some perceptible variability in depth. Error bars ± 1 SEM. (a) In the haptic-for-texture condition, the relative influence of texture information increased from Pre-test to Post-test; stereo settings are higher at left and lower at right. These data show that after Grasp training, stronger stereo signals were required to balance out the same weak texture signals (18 and 24 mm) and make them equivalent to the 30-mm cue-consistent standard, while weaker stereo signals were required to balance out the same strong texture signals (36 and 42 mm). (b) No perceptual change was observed in the haptic-for-stereo condition; stereo settings were the same in Pre-test and Post-test.

a total of 27 trails. In the Adaptation phase, we presented five cue-conflict objects with a constant 8-mm difference between texture depths (18, 24, 30, 36, and 42 mm) and stereo depths (10, 16, 22, 28, and 36 mm). Haptic depth always matched texture depth in Experiment 2. Participants grasped these five objects over 21 bins for a total of 105 Adaptation trials.

2.4. Analysis

Raw motion-capture position data was processed and analyzed offline using custom software. Missing frames due to marker dropout were linearly interpolated, and the 85-Hz raw data was smoothed with a 20-Hz low-pass filter. The grip aperture profile was computed for each trial by taking the Z-distance between the index finger and thumb locations on each frame (*i.e.*, the fingers' separation in depth, along the sagittal axis). We used this measure rather than the standard 3D vector distance between the fingertips because we found it slightly reduced the variance of our MGA slope estimates (described below), perhaps by factoring out motor noise in the vertical separation between the index finger and thumb, which is unrelated to object depth. The maximum grip aperture (MGA) was extracted from this time series. We excluded three out of 9432 trials in Experiment 1, and five out of 2640 trials in Experiment 2, where missing data from Optotrak marker occlusions made it impossible to extract a valid maximum grip aperture.

The relative cue weights in the Pre-test and Post-test were computed based on the stereo and texture settings for the four cue-conflict metamers. Since the cue-consistent standard was 30 mm in depth, stereo weight $w_S = (30 - z_T)/(z_S – z_T)$, where z_T and z_S denote, respectively, the fixed texture depth and the final stereo setting. This equation assumes that perceived depth is a weighted linear combination of stereo and texture depth with sum-to-one weights, so texture weight $w_T = 1 – w_S$.

To analyze the grasping data of Experiment 1, we regressed the MGAs in each bin against the texture depths to obtain MGA scaling across the metamers (see Fig. 3). To analyze the correlation between perceptual and motor changes, for each participant we transformed the measured perceptual change into a prediction of the MGA scaling across the metamers: $k_{metamers} = ((1 - w_{SPost}) – (1 - w_{SPre}))/w_{SPre})$, where w_{SPre} and w_{SPost} are the stereo weights in Pre-test and Post-test, and $k_{metamers}$ is the predicted MGA scaling across the metamers. The Pre-test stereo weight appears in the denominator because it determines the maximum possible increase in texture weight. Empirical MGA slopes were computed by regressing the average MGAs from the Adaptation phase against the texture depths of the metamers. In Experiment 2, we predicted the decrease in the average MGA at the beginning of the Adaptation phase by multiplying the Pre-test stereo weight by the imposed 8-mm decrease in stereo depth, then subtracting this value from the average MGA in the final Baseline bin. To statistically analyze the results, we performed planned, hypothesis-driven comparisons (one-tailed *t*-tests; $\alpha = 0.05$) to determine whether (a) MGA slopes showed a significant positive or negative linear trend over the course of Adaptation in Experiment 1, (b) the perceptual weights changed in the expected direction from Pre-test to Post-test Metamer Matching, (c) across individuals, MGA slopes during Adaptation were correlated with perceptual reweighting, and (d) the perceptual reweighting in Experiment 2 was greater than in Experiment 1.

3. Results

3.1. Pre-test metamer matching results

Pre-test results are depicted in Fig. 3 (black closed circles and dotted lines; colored open circles and solid lines depict the Post-test results, described later). For each of the four texture depths (18, 24, 36, or 42 mm), participants adjusted stereo depth until the resulting cue-conflict stimulus perceptually matched the 30-mm cue-consistent standard. In the haptic-for-texture condition, those four texture depths were paired, respectively, with stereo depths of 36.9, 32.1, 26.1, and 23.1 mm (SEMs: 1.1, 0.5, 0.6, 1.0 mm), indicating a texture weight of 0.270 (SEM = 0.026). In the haptic-for-stereo condition, the adjusted stereo depths were 36.5, 31.7, 26.2, and 22.6 mm (SEMs: 1.1, 0.5, 0.5, 0.9 mm), indicating a texture weight of 0.263 (SEM = 0.029). Nearly equivalent Pre-test settings across conditions make sense, as no visuomotor training was yet provided.

As expected, stereo depth settings were inversely related to the fixed texture depths: stereo settings were largest for the smallest texture depth, and smallest for the largest texture depth. The haptic feedback provided in the grasping task was therefore positively correlated with

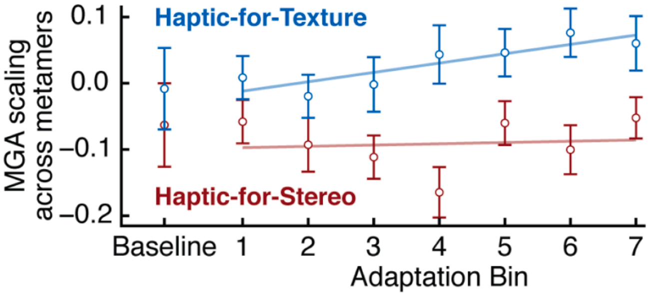

Fig. 4. Experiment 1 grasping results. Timeline of MGA scaling across the metamer set, defined as the slope of the MGA with respect to texture depth. Error bars ± 1 SEM. Since texture was negatively correlated with stereo for the metamers, a positive slope indicates that the MGA scaled with texture, while a negative slope indicates scaling with stereo. When metamers were first introduced (Baseline), MGA slopes were near zero, mirroring the perceptual equivalence. Across the Adaptation phase, positive-trending slopes were observed in the haptic-for-texture condition, indicating increased reliance on texture. However, negative-trending slopes, which would indicate increased reliance on stereo, were not observed in the haptic-for-stereo condition.

one cue (the reinforced cue) and negatively correlated with the other (the faulty cue). Note, however, that we opted to include additional stimuli in the grasping task in order to provide some variation in perceived depth. Our reasoning was that if all the stimuli were perceived to be equal in depth, participants may give up trying to scale their grip apertures with the objects. So, to provide some perceptible variability in depth that remained positively correlated with haptic feedback, we replicated the set of five metamers specified by each participant in the Pre-test to create three distinct sets (gray circles and dotted lines in Fig. 3; see Appendix for details).

3.2. Grasping results

In the Pre-Baseline phase, MGAs reliably scaled with variations in cue-consistent depths (slope = 0.64, SEM = 0.05; not depicted in Fig. 4). In the Baseline phase, we introduced the five depth metamers from Pre-test, but paired them all with 30-mm haptic feedback in order to measure grasp performance before reinforcing either cue. As predicted, participants used roughly the same MGA across the metamers, mirroring the perceptual equivalence of these stimuli (Fig. 4); MGA scaling with texture was −0.01 in haptic-for-texture and −0.06 in haptic-for-stereo (both SEM = 0.06). In contrast, if grasp planning depended on separate 3D shape processing than perception, with greater weight on stereo information (cf. Knill, 2005; Goodale, 2011), these slopes should have been significantly negative. This result demonstrates that depth metamers elicit indistinguishable visuomotor responses despite their differing combinations of stereo and texture information.

In the Adaptation phase, participants grasped the full set of metamers (the fifteen black and gray solid points in Fig. 3), with haptic feedback that was positively correlated with one cue and negatively correlated with the other. Cue reweighting in the haptic-for-texture condition would be shown by the MGA slope with texture becoming gradually more positive, while in the haptic-for-stereo condition it would be shown by the MGA slope with texture becoming gradually more negative (remember the cues are inversely correlated, so a negative slope with texture entails a positive slope with stereo). In the haptic-for-texture condition, we found a positive linear trend in the MGA slopes with texture across the seven Adaptation bins ($t(35) = 2.76$, $p = 0.0046$). However, despite the negative-trending MGA slopes seen in the first four Adaptation bins, the haptic-for-stereo condition failed to produce a stable negative trend in the MGA slope with texture across all seven bins ($p = 0.63$). Although the MGA slope was already negative at the start of Adaptation, possibly due to some imprecise Pre-test metamer matching, there is no reason to believe that this is why the MGA slopes did not maintain a stable negative trend.

This asymmetry in cue reweighting continues a surprising trend that has emerged in our recent work (Cesanek & Domini, 2019): haptic-for-stereo conditions consistently elicit milder reweighting than haptic-for-texture conditions. The reasons for this remain unclear, but there are a few tenable hypotheses to explore. Perhaps the most obvious suggestion is that the asymmetry has to do with the different feedback patterns across conditions. In this experiment, due to our metamer-based approach, the variability in stereo depth (14 mm) was about half the variability in texture depth (24 mm) during the Adaptation phase, providing a much smaller range of stereo depths over which error feedback was experienced. At the same time, due to noise in the matching process and the procedure for creating the augmented set of metamers (see Appendix), the correlation between stereo and haptic depths was arguably weaker in the haptic-for-stereo condition than is normally experienced in reality.

Another (non-mutually exclusive) possibility is that the asymmetry may actually indicate that our results are due to sensory recalibration, rather than reweighting (Adams et al., 2010; Block & Bastian, 2011). For instance, the observed cue reweighting in the haptic-for-texture condition may actually reflect a gain reduction in stereo processing *prior* to cue combination, where the same binocular disparities are re-mapped onto a smaller range of depth estimates. If so, perhaps the extremely low correlation between haptic feedback and stereo depth reduced the gain on stereo information, while the merely moderate positive correlation in the haptic-for-stereo condition failed to increase the gain, which would make sense given the strong correlation experienced in reality. Conversely, perhaps a similar perceptual gain on texture processing was increased in the haptic-for-stereo condition due to the strong positive correlation with haptic feedback (note that, in reality, texture is not nearly as strongly correlated with physical shape as stereo), with no change in stereo processing. Although these hypotheses are merely speculative, they suggest important future avenues for investigations of perceptual and motor cue reweighting, and underscore the fact that the present results cannot discriminate between cue reweighting and cue recalibration.

3.3. Post-test metamer matching results

The main aim of this study was to demonstrate that changes in grasping performance are related to upstream changes in the weighting of depth cues for perceptual judgments. Returning to Fig. 3, we now evaluate changes in the stereo settings from Pre-test (solid circles, dotted lines) to Post-test (open circles, solid lines) as evidence of perceptual cue reweighting. In the haptic-for-texture condition (Fig. 3a), the Post-test texture weight was 0.308 (SEM = 0.032), up about 4% from the Pre-test value of 0.270. In the haptic-for-stereo condition (Fig. 3b), the relative weight of texture information was 0.259 (SEM = 0.031), a small decrease from the value of 0.263 measured in the Pre-test. Most importantly, these changes in cue weights were found to be significantly modulated by feedback condition ($t(35) = 1.77$, $p = 0.043$). Follow-up t-tests revealed significant perceptual reweighting in the haptic-for-texture condition ($\Delta w_{stereo} = -0.038$, $t(35) = -2.43$, $p = 0.010$), but not in the haptic-for-stereo condition ($\Delta w_{stereo} = 0.004$, $t(35) = 0.20$, $p = 0.42$).

The main goal of this experiment was to determine whether perceptual and visuomotor cue reweighting are driven by modification of a shared cue-combination function, as opposed to being to independent types of learning. Since our haptic-for-stereo condition was ineffective in eliciting either type of cue reweighting, it is more consistent with our hypothesis than if we had found reweighting in only one task, yet these null findings do not allow any stronger conclusion. On the other hand, we observed both perceptual and visuomotor cue reweighting in the haptic-for-texture condition. Thus, we analyzed this condition to determine whether perceptual changes were correlated with grasping performance across individual participants, which would

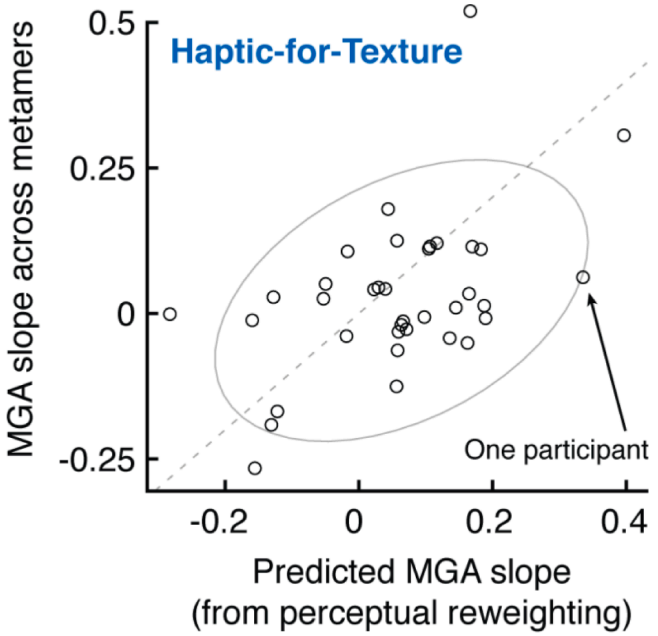

Fig. 5. Individual perceptual changes predict grasp performance during Adaptation. In the haptic-for-texture condition, where we found both motor and perceptual reweighting, predicted MGA slopes across the five metamers (based on their measured perceptual change) were correlated with actual slopes. Ellipse is 95% confidence region; dashed line is unity.

suggest a common source. This analysis produced the key result of this study: individual perceptual changes, converted into predictions of MGA slope during Adaptation, were significantly correlated with the measured MGA slopes (Pearson's $r = 0.49$, $t(34) = 3.30$, $p = 0.0023$; Fig. 5).

3.4. *Experiment 2: Constant bias in stereo*

If the perceptual cue reweighting observed in Experiment 1 was the result of variable movement errors, then perceptual changes should not occur during exposure to a biased cue, since constant movement errors can be resolved rapidly by sensorimotor adaptation. To test this prediction, we ran a control experiment with twenty new participants. The design was similar to the haptic-for-texture condition of Experiment 1, except we did not present the metamers indicated in the Pre-test as grasping stimuli. Instead, at the transition from Baseline (cue-consistent stimuli only) to Adaptation, we introduced a fixed cue-conflict: the stereo depths (10–34 mm in 6-mm increments) were always 8 mm shallower than the corresponding texture depths (18–42 mm), while haptic feedback reinforced texture.

Fig. 6a shows that when stereo depths decreased by 8 mm at the onset of Adaptation, the MGA suddenly dropped by 5.75 mm. This change in the motor response matches what we would have predicted based solely on the perceptual cue weights measured in the Pre-test (see prediction interval in Fig. 6a, bin 4), again indicating that weights are the same in perception as in action. Subsequently, MGAs increased and leveled off near their Baseline values, fully compensating for the biased stereo cue. The time course of MGAs was well captured by an exponential fit (adjusted $R^2 = 0.58$), consistent with the proportional error-correction model of sensorimotor adaptation. However, there is a slight deviation from the standard adaptation curve in bins 9–10, where the MGA suddenly decreases, then gradually resumes smoothly increasing to the plateau. This deviation causes the plateau of the fitted exponential to undershoot the final MGA. We suspect this behavior is due to sudden changes in grasping strategy. Although we instructed participants to reach for the objects rapidly and naturally, as they would in everyday grasping, it would not be surprising if some individuals responded to the suddenly introduced size discrepancy by immediately adopting a "probing" grasp strategy with larger MGAs. This fast, explicit strategy shift would explain the rapid corrections seen in bins 5–8 (Smith, Ghazizadeh, & Shadmehr, 2008; Taylor, Krakauer, & Ivry, 2014; McDougle, Bond, & Taylor, 2015). After quickly reducing errors to a more comfortable level, subjects may have switched back to the instructed, natural grasping strategy in bins 9–10, showing gradual error correction thereafter.

Unlike in Experiment 1, texture weight did not increase from Pre-test to Post-test; rather, it slightly decreased from 0.246 to 0.240 ($p = 0.63$; Fig. 6b). Moreover, the perceptual reweighting measured in Experiment 1 was significantly greater than that in Experiment 2 (Welch's two-sample *t* test; $t(41.855) = 1.78$, $p = 0.041$; Fig. 6c), despite the approximately equivalent exposure to visual-haptic mismatches in both experiments, in terms of number of trials and average magnitude of the mismatches.

4. Discussion

Our experiments show that when an unreliable depth cue is given undue influence in motor planning, the variable motor errors that result during manual interactions can produce depth cue reweighting in both perception and action. Meanwhile, when motor errors from a biased depth cue can be resolved by rapid motor recalibration, cue reweighting does not occur. These results connect previous studies that show perceptual cue reweighting contingent on haptic feedback (Atkins et al., 2001; Ernst et al., 2000) with those showing motor cue reweighting across repeated object-directed actions (van Beers et al., 2011; Cesanek & Domini, 2019). Rather than being two separate learning processes with different computational goals, the observed cue reweighting in motor behavior seems to be linked to upstream perceptual reweighting, since perceptual cue reweighting was correlated with grasping performance in Experiment 1. This relationship supports the idea that depth cue processing is the same for action and for perception, in contrast to the dissociated view of these functions (*cf.* Knill, 2005; Goodale, 2011). A common cue-combination function for perception and action is also supported by the fact that participants did not scale their maximum grip apertures across the metamers when they were first introduced in Experiment 1, showing that the perceptual equivalence of these stimuli caused them to be treated as such in grasp planning. Furthermore, in Experiment 2, suddenly reducing the stereo depth caused an immediate change in the maximum grip aperture that was consistent with the perceptual weight of stereo.

Previous studies of feedback-based depth cue reweighting have emphasized cross-modal comparison of haptic information and single-cue estimates of 3D shape, suggesting a purely perceptual learning process. However, all of these studies were designed using stimulus sets where one depth cue was manipulated to be less correlated with physical object shape. In the Introduction, we described how persistent, variable errors occur as a direct consequence of reducing a depth cue's correlation with physical shape. This observation led us to propose that persistent movement errors are a strong driving signal in feedback-based cue reweighting. Consistent with this proposal, we have previously shown that cue reweighting in a motor task does not occur during exposure to a constant bias, but only in response to reduced correlation of one available cue with haptic feedback (Cesanek & Domini, 2019). Likewise, in the present study, perceptual cue reweighting occurred when haptic feedback was negatively correlated with stereo (Exp. 1), but not when haptic feedback was simply misaligned with stereo by a constant offset (Exp. 2). In the biased-stereo condition, sensorimotor adaptation drove the motor response toward the physical surface shape, rapidly compensating for the perceptual bias. Thus, consistent with our previous work on motor reweighting of depth cues, it appears that perceptual reweighting is not driven by the absolute mismatch between each cue and haptic feedback, but depends on altered correlations

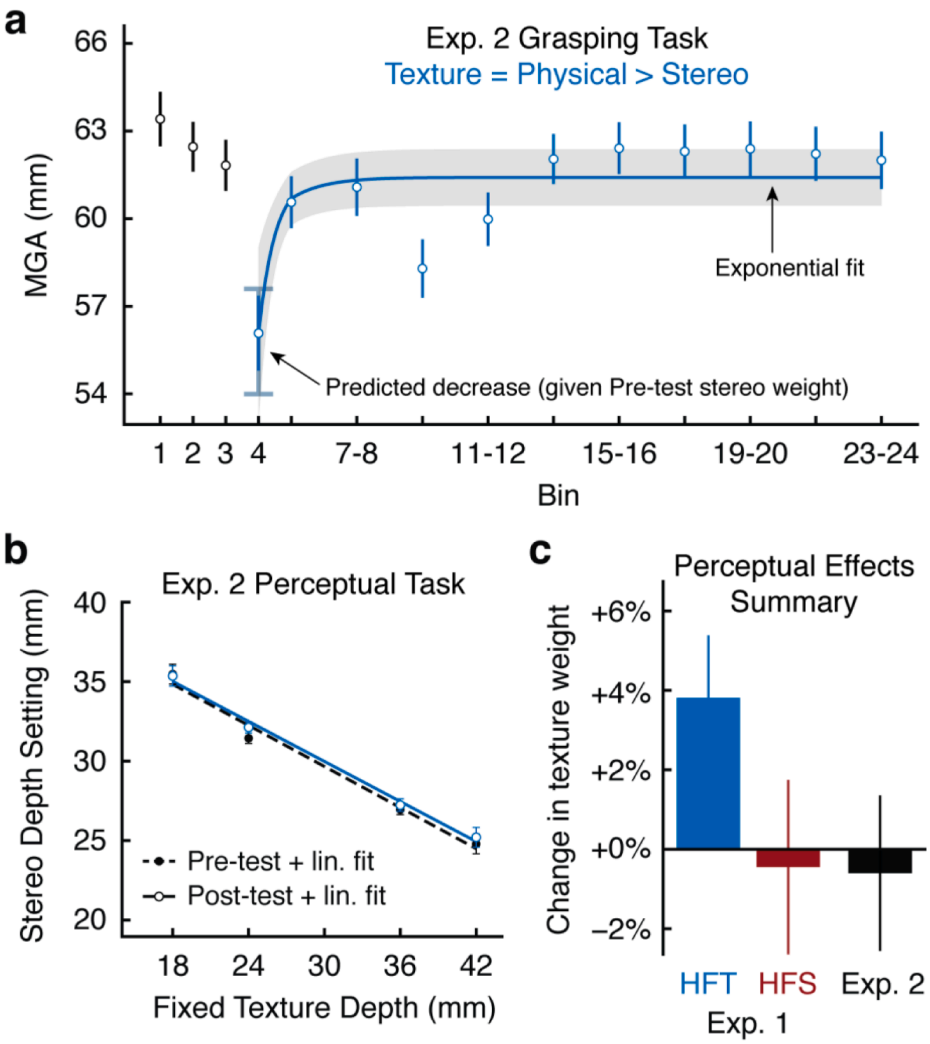

Fig. 6. Experiment 2 results and comparison with Experiment 1. (a) Stereo depth was suddenly decreased by 8 mm at the transition from Baseline (black circles) to Adaptation (blue circles). MGAs immediately decreased by 5.75 mm, matching a prediction based on the Pre-test stereo weight of 0.75 (light blue interval in bin 4; ±1 SEM). In the Adaptation phase, MGAs returned to Baseline levels following an exponential function (blue fit line). (b) No changes were observed in the metamer stereo settings from Pre-test to Post-test. (c) Summary of the perceptual effects from Experiments 1 and 2. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

between individual depth cues and haptic feedback. Although it is possible that these purely sensory correlations are tracked and used as a proxy for cue reliability when determining weights, we speculate that movement errors are the driving force behind reweighting. Altered correlations are necessary only because they give rise to persistent, systematic movement errors, and an accumulation of repeated errors may be necessary to produce noticeable changes in a slow-to-adapt perceptual process.

It is informative to compare the present findings with previous work on visual-proprioceptive reweighting in target-directed reaching tasks. Consistent with our findings, visual-proprioceptive reweighting is quite slow in paradigms similar to our own, which introduce altered correlations between error signals and the sensory inputs, thwarting standard motor adaptation (*e.g.*, the "error variance" manipulation of Block & Bastian, 2010). However, this literature also shows that cue reweighting and recalibration are not always slow, as dramatic shifts in the relative weight of proprioception for hand localization can also be obtained almost instantaneously (*e.g.*, "visual capture" in Mon-Williams, Wann, Jenkinson, & Rushton, 1997; the "conscious effort" manipulation of Block & Bastian, 2010). In contrast to the present findings, such instances of rapid reweighting appears to involve either (a) classic "dynamic cue weighting" based on the reliability of the input signals (Maloney & Landy, 1989; Ghahramani et al., 1997; Ernst & Banks, 2002) or (b) individuals selectively attending to the visual or the proprioceptive input, which are consciously separable. In contrast, explicit isolation of individual depth cues is extremely difficult, if not impossible, in 3D shape perception. Indeed, the phenomenon of "mandatory fusion" of stereo and texture cues to slant, but not of visual and proprioceptive cues to size, was specifically demonstrated by Hillis, Ernst, Banks, & Landy (2002). This difference is quite intuitive given that stereo and texture cues are, by necessity, always observed together on a stimulus (as pictorial features are necessary for binocular fusion), while proprioception of a limb frequently occurs without vision of the limb. Additionally, visual-proprioceptive misalignments are a standard problem that the sensorimotor system must resolve to enable flexible manipulation of tools. Therefore, perhaps the availability of a "misalignment error" signal between simultaneous visual and proprioceptive estimates of hand position, which is not available for mandatorily fused stereo and texture estimates of object depth, could explain why proprioceptive recalibration is observed in standard motor adaptation paradigms (Block & Bastian, 2011; Henriques & Cressman, 2012; Mostafa, Kamran-Disfani, Bahari-Kashani, Cressman, & Henriques, 2015; Ostry & Gribble, 2016), whereas we found no evidence of stereo or texture recalibration in Experiment 2. Furthermore, this hypothesized misalignment signal would also explain why proprioceptive recalibration can occur even in cerebellar patients (Block and Bastian, 2012; Henriques et al., 2014), who presumably do not have access to the type of movement error signals that we propose are responsible for feedback-based cue reweighting.

One possible mechanism of feedback-based cue reweighting is that the perceptual changes are driven by sensory-prediction errors, the same types of signals that drive other forms of motor learning (Shadmehr

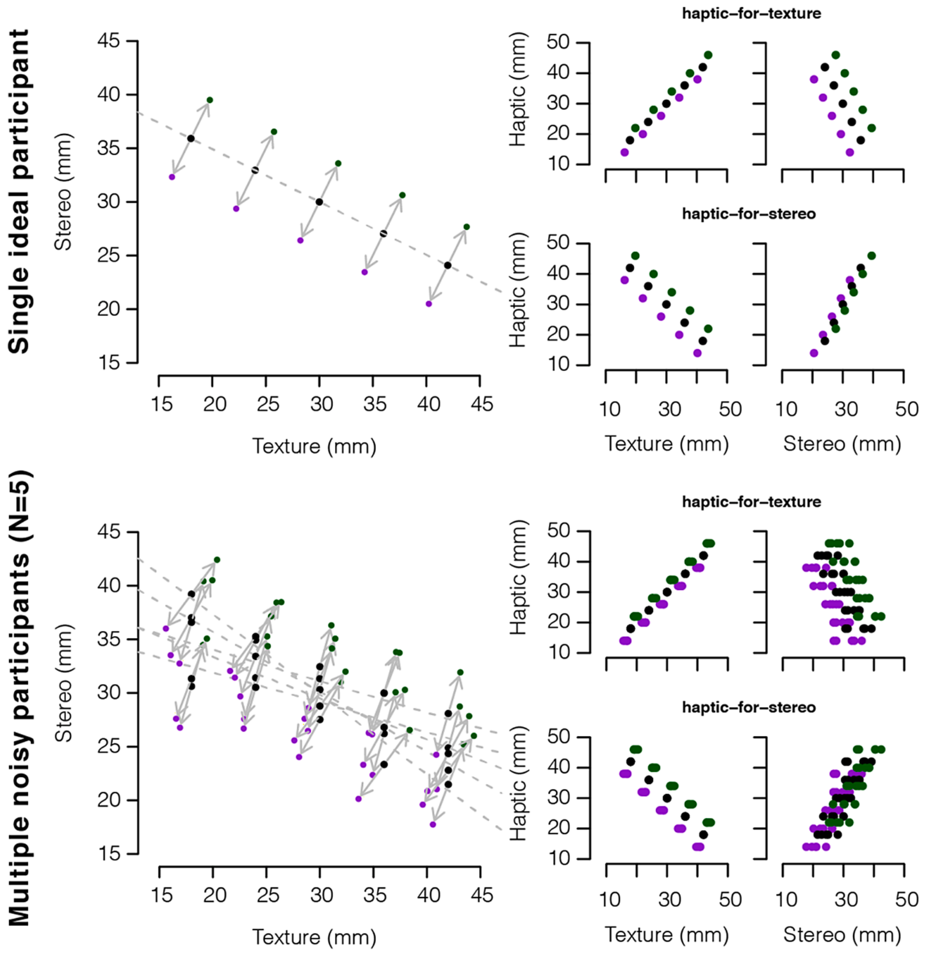

Fig. A1. Simulated joint distributions of sensory inputs in the augmented metamer set. Upper: At left, augmented set of stereo-texture depth metamers for a observer with texture weight of 0.33 (black dots, noiseless Pre-test metamer matches; green and purple dots, augmented set formed by locally shifting the Pre-test matches). At right, the joint distributions of sensory cues and haptic feedback in each condition of Experiment 1 (haptic-for-stereo and haptic-for-texture). The haptic feedback was the same for all participants, and the values were the same in both conditions. Lower: Same as the upper panel, but for 5 simulated participants with between-subject noise in texture weight, and within-subject noise in the adjusted stereo values of the Pre-test metamer matches. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

et al., 2010), as opposed to a passive sensory process that monitors the covariance of different sensory modalities. Support for this idea can be found in a study from Adams et al. (2010), who showed that perceptual processing of shading cues changed gradually over repeated interactions where observers viewed a shading-only stimulus, then briefly received conflicting haptic or stereo information. The sensory feedback thus violated the observer's predictions about what that feedback should have looked or felt like, which were formed on the basis of shading alone. However, in another condition, observers viewed conflicting shading and stereo information from the start of the trial, and briefly received haptic feedback that conflicted with shading but was consistent with stereo. Here, perceptual changes were greatly reduced, despite the presence of the same mismatch between shading and stereo, and between shading and haptic feedback. The key difference is that the cue-combined percept was now dominated by stereo information, so the haptic feedback was more consistent with the observer's predictions than in the original condition, thus generating a smaller error signal. The authors referred to the critical element for producing perceptual changes as an "oops factor", where the new sensory signals forced a revision of the initial percept (Adams et al., 2010). In our view, this is essentially the same concept as a sensory-prediction error: a conflict between actual sensory feedback and an internal prediction of that feedback formed on the basis of prior information. Therefore, these findings are consistent with our proposal that sensory-prediction errors may be involved not only in motor learning, but also in perceptual learning.

However, registering sensory-prediction errors is not enough to produce visual perceptual changes—the second piece of our proposal is that these errors must be persistent. When errors are rapidly eliminated, for instance by sensorimotor adaptation, visual perceptual changes do not seem to occur (see Exp. 2). In contrast, studies that have succeeded in eliciting perceptual changes in depth cue processing have always involved persistent sensory-prediction errors. As mentioned earlier, all previous studies on depth cue reweighting (Atkins et al., 2001; Ernst et al., 2000; Ho et al., 2009) used a stimulus set where the correlation between one depth cue and haptic feedback was reduced, leading to persistent variable errors. Likewise, studies examining the perceptual recalibration of a single depth cue have also involved persistent, variable errors. For the bump/dimple stimuli used by Adams et al. (2010), only some targets were paired with feedback that conflicted with the initial shading cue, and even within this small subset the direction of the errors varied: exploration of some perceived dimples ended up generating feedback consistent with a bump, and some perceived bumps generated feedback consistent with a dimple. In another experiment investigating perceptual recalibration of depth-from-stereo (Experiment 1 of Atkins et al., 2003), participants grasped stereo-only objects along their depth dimension, with haptic feedback that was always deeper than the stereo depth. However, due to the specifics of their experimental design (see their Equation 1), the visual-haptic mismatches for the training stimuli spanned a range of 14.7 mm: from − 8.8 mm (when a 32-mm stereo stimulus viewed from 465 mm was paired with 40.8-mm haptic feedback at a reaching distance of 525 mm) to −23.5 mm (when a 68-mm stereo stimulus viewed at 375 mm was paired with 91.5-mm haptic feedback at a reaching distance of 435 mm). Thus, despite the haptic feedback being consistently deeper than the stereo depths, variable errors still would have prevented sensorimotor adaptation from fully eliminating sensory-prediction errors.

More recently, neurophysiological studies have provided evidence that visual processing can be affected by persistent error signals in visuomotor tasks. Kojima and Soetedjo (2017) found that firing rates of superior colliculus neurons, believed to encode a visual spatial map of egocentric location, were reduced over time in a saccade adaptation task where a persistent visual error of 4° was induced over hundreds of trials. Although saccade control and egocentric location perception undoubtedly involve a different set of neural mechanisms than grasp control and 3D shape perception, it is encouraging to see that similar principles may apply across domains. Indeed, Zimmermann and Lappe (2016) have endorsed a similar position to our own, pointing out that perceptual shifts in 2D target localization following saccade adaptation appear to require large, persistent error signals. In summary, the common thread across multiple studies, including the present one, is that changes in visual perception occur precisely in those situations where sensory-prediction errors are highly variable, and therefore persistent, since variable errors cannot be resolved by classic downstream motor adaptation.

5. Appendix

The procedure for creating the grasp adaptation stimuli in Experiment 1 involves augmenting the set of metamers created in the Pre-test by matching to the 30-mm cue-consistent standard. Additionally, the haptic feedback provided during the Adaptation phase was fixed across participants, regardless of the stereo settings they produced for the Pre-test metamer matches. This gives rise to patterns of correlation between the sensory cues and the haptic feedback across the two conditions (haptic-for-stereo and haptic-for-texture) that are not intuitive. In Fig. A.1, we provide an illustration of the correlations between haptic feedback and the available stereo/texture cues in the two conditions of Experiment 1. In the top-left panel, we simulate the Pre-test metamer matches of an observer with a texture weight of 0.33 (black dots). The augmented stimulus set used for grasp adaptation in Experiment 1 included 10 additional stimuli generated by shifting the matched set of metamers +/−4 mm perpendicular to the linear regression line through the Pre-test metamers, in stereo-texture space (green and purple dots). At right, we show how the stereo and texture values of the augmented stimulus set, for this simulated participant, are jointly distributed with the haptic feedback provided in the grasp adaptation phase, which was the same for all participants. As shown by the figures at right, there are four distinct patterns of correlation with haptic feedback, across the two cues (texture and stereo) and the two conditions (haptic-for-texture and haptic-for-stereo). In the lower, we display the distributions of augmented-set stimuli created by simulating 5 noisy subjects, with between-subject noise in the texture weight and within-subject noise in the adjusted stereo values of the Pre-test metamer set.

CRediT authorship contribution statement

Evan Cesanek: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing - original draft, Writing - review & editing. **Jordan A. Taylor:** Conceptualization, Writing - review & editing, Visualization, Supervision, Funding acquisition. **Fulvio Domini:** Conceptualization, Methodology, Resources, Writing - review & editing, Supervision, Funding acquisition.

Acknowledgment

This work was supported by a National Science Foundation grant to FD and JAT (BCS-1827550).

References

Adams, W. J., Banks, M. S., & van Ee, R. (2001). Adaptation to three-dimensional distortions in human vision. *Nature Neuroscience, 4*(11), 1063–1064.

Adams, W. J., Kerrigan, I. S., & Graf, E. W. (2010). Efficient visual recalibration from either visual or haptic feedback: The importance of being wrong. *The Journal of Neuroscience, 30*(44), 14745–14749.

Atkins, J. E., Fiser, J., & Jacobs, R. A. (2001). Experience-dependent visual cue integration based on consistencies between visual and haptic percepts. *Vision Research, 41*(4), 449–461.

Atkins, J. E., Jacobs, R. A., & Knill, D. C. (2003). Experience-dependent visual cue recalibration based on discrepancies between visual and haptic percepts. *Vision Research, 43*(25), 2603–2613.

Bingham, G. P., Crowell, J. A., & Todd, J. T. (2004). Distortions of distance and shape are not produced by a single continuous transformation of reach space. *Perception & Psychophysics, 66*(1), 152–169.

Block, H. J., & Bastian, A. J. (2010). Sensory reweighting in targeted reaching: Effects of conscious effort, error history, and target salience. *Journal of Neurophysiology, 103*, 206–217.

Block, H. J., & Bastian, A. J. (2011). Sensory weighting and realignment: Independent compensatory processes. *Journal of Neurophysiology, 106*, 59–70.

Block, H. J., & Bastian, A. J. (2012). Cerebellar involvement in motor but not sensory adaptation. *Neuropsychologia, 50*, 1766–1775.

Cesanek, E., & Domini, F. (2017). Error correction and spatial generalization in human grasp control. *Neuropsychologia, 106*, 112–122.

Cesanek, E., & Domini, F. (2019). Depth cue reweighting requires altered correlations with haptic feedback. *Journal of Vision, 19(14), 3*, 1–13.

Cesanek, E., Taylor, J. A., & Domini, F. (2020). Sensorimotor adaptation and cue reweighting compensate for distorted 3D shape information, accounting for paradoxical perception-action dissocations. *Journal of Neurophysiology, 123*, 1407–1419.

Domini, F., & Caudek, C. (2003). 3-D structure perceived from dynamic information: A new theory. *Trends in Cognitive Sciences, 7*(10), 444–449.

Domini, F., & Caudek, C. (2010). Matching perceived depth from disparity and from velocity: Modeling and psychophysics. *Acta Psychologica, 133*, 81–89.

Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature, 415*, 429–433.

Ernst, M. O., Banks, M. S., & Bülthoff, H. H. (2000). Touch can change visual slant perception. *Nature Neuroscience, 3*(1), 69–73.

Ghahramani, Z., Wolpert, D. M., & Jordan, M. I. (1997). Computational models for sensorimotor integration. In P. G. Morasso, & V. Sanguineti (Eds.), *Self-Organization, Computational Maps and Motor Control* (pp. 117–147). Amsterdam: North-Holland.

Goodale, M. A. (2011). Transforming vision into action. *Vision Research, 51*(13), 1567–1587.

Harris, C. S. (1965). Perceptual adaptation to inverted, reversed, and displaced vision. *Psychological Review, 72*(6), 419–444.

Held, R., & Hein, A. V. (1958). Adaptation of disarranged hand-eye coordination contingent upon re-afferent stimulation. *Perceptual and Motor Skills, 8*(3), 87–90.

Henriques, D. Y. P., & Cressman, E. K. (2012). Visuomotor adaptation and proprioceptive recalibration. *Journal of Motor Behavior, 44*, 435–444.

Henriques, D. Y. P., Filippopulos, F., Straube, A., & Eggert, T. (2014). The cerebellum is not necessary for visually driven recalibration of hand proprioception. *Neuropsychologia, 64*, 195–204.

Hillis, J. M., Ernst, M. O., Banks, M. S., & Landy, M. S. (2002). Combining sensory information: Mandatory fusion within, but not between, senses. *Science, 298*, 1627–1630.

Hillis, J. M., Watt, S. J., Landy, M. S., & Banks, M. S. (2004). Slant from texture and disparity cues: Optimal cue combination. *Journal of Vision, 4*(12), 967–992.

Ho, Y.-X., Serwe, S., Trommershäuser, J., Maloney, L. T., & Landy, M. S. (2009). The role of visuohaptic experience in visually perceived depth. *Journal of Neurophysiology, 101*(6), 2789–2801.

Johnston, E. B. (1991). Systematic distortions of shape from stereopsis. *Vision Research, 31*(7–8), 1351–1360.

Knill, D. C. (2005). Reaching for visual cues to depth: The brain combines depth cues differently for motor control and perception. *Journal of Vision, 5*(2), 103–115.

Knill, D. C., & Saunders, J. A. (2003). Do humans optimally integrate stereo and texture information for judgments of surface slant? *Vision Research, 43*(24), 2539–2558.

Kojima, Y., & Soetedjo, R. (2017). Change in sensitivity to visual error in superior colliculus during saccade adaptation. *Scientific Reports, 7*, 9566.

Maloney, L. T., & Landy, M. S. (1989). A statistical framework for robust fusion of depth information. *Visual Communications and Image Processing IV*. https://doi.org/10.1117/12.970125.

McDougle, S. D., Bond, K. M., & Taylor, J. A. (2015). Explicit and implicit processes constitute the fast and slow processes of sensorimotor learning. *The Journal of Neuroscience, 35*(26), 9568–9579.

Mon-Williams, M., Wann, J. P., Jenkinson, M., & Rushton, K. (1997). Synaesthesia in the normal limb. *Proceedings of the Royal Society B, 264*, 1007–1010.

Mostafa, A. A., Kamran-Disfani, R., Bahari-Kashani, G., Cressman, E. K., & Henriques, D. Y. P. (2015). Generalization of reach adaptation and proprioceptive recalibration at different distances in the workspace. *Experimental Brain Research, 233*, 817–827.

Norman, J. F., Farley Norman, J., Todd, J. T., Perotti, V. J., & Tittle, J. S. (1996). The visual perception of three-dimensional length. *Journal of Experimental Psychology: Human Perception and Performance, 22*(1), 173–186.

Norman, J. F., Lappin, J. S., & Norman, H. F. (2000). The perception of length on curved and flat surfaces. *Perception & Psychophysics, 62*(6), 1133–1145.

Ostry, D. J., & Gribble, P. L. (2016). Sensory plasticity in human motor learning. *Trends in Neurosciences, 39*(2), 114–123.

Redding, G. M., & Wallace, B. (1997). *Adaptive Spatial Alignment*. Mahwah, NJ: Lawrence Erlbaum Associates, Publishers.

Shadmehr, R., Smith, M. A., & Krakauer, J. W. (2010). Error correction, sensory prediction, and adaptation in motor control. *Annual Review of Neuroscience, 33*, 89–108.

Smeets, J. B., van den Dobbelsteen, J. J., de Grave, D. D., van Beers, R. J., & Brenner, E. (2006). Sensory integration does not lead to sensory calibration. *Proceedings of the National Academy of Sciences of the United States of America, 103*(49), 18781–18786.

Smith, M. A., Ghazizadeh, A., & Shadmehr, R. (2006). Interacting adaptive processes with different timescales underlie short-term motor learning. *PLoS Biology, 4*(6), 1035–1043.

Taylor, J. A., Krakauer, J. W., & Ivry, R. B. (2014). Explicit and implicit contributions to learning in a sensorimotor adaptation task. *The Journal of Neuroscience, 34*(8), 3023–3032.

van Beers, R. J., van Mierlo, C. M., Smeets, J. B. J., & Brenner, E. (2011). Reweighting visual cues by touch. *Journal of Vision, 11*(10), 20.

von Helmholtz, H. (1962). Treatise on Physiological Optics. In J. P. Southall, Ed. & Trans. New York; Dover.

Welch, R. B. (2013). *Perceptual Modification: Adapting to Altered Sensory Environments*. New York: Academic Press.

Young, M. J., Landy, M. S., & Maloney, L. T. (1993). A perturbation analysis of depth perception from combinations of texture and motion cues. *Vision Research, 33*(18), 2685–2696.

Zimmermann, E., & Lappe, M. (2016). Visual space constructed by saccade motor maps. *Frontiers in Human Neuroscience, 10*, 225.