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**RESEARCH ARTICLE** | *Control of Movement*

# Sensorimotor adaptation and cue reweighting compensate for distorted 3D shape information, accounting for paradoxical perception-action dissociations

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**Cesanek E, Taylor JA, Domini F.** Sensorimotor adaptation and cue reweighting compensate for distorted 3D shape information, accounting for paradoxical perception-action dissociations. *J Neurophysiol* 123: 1407–1419, 2020. First published February 26, 2020; doi:10.1152/jn.00718.2019.—Visually guided movements can show surprising accuracy even when the perceived three-dimensional (3D) shape of the target is distorted. One explanation of this paradox is that an evolutionarily specialized “vision-for-action” system provides accurate shape estimates by relying selectively on stereo information and ignoring less reliable sources of shape information like texture and shading. However, the key support for this hypothesis has come from studies that analyze average behavior across many visuomotor interactions where available sensory feedback reinforces stereo information. The present study, which carefully accounts for the effects of feedback, shows that visuomotor interactions with slanted surfaces are actually planned using the same cue-combination function as slant perception and that apparent dissociations can arise due to two distinct supervised learning processes: sensorimotor adaptation and cue reweighting. In two experiments, we show that when a distorted slant cue biases perception (e.g., surfaces appear flattened by a fixed amount), sensorimotor adaptation rapidly adjusts the planned grip orientation to compensate for this constant error. However, when the distorted slant cue is unreliable, leading to variable errors across a set of objects (i.e., some slants are overestimated, others underestimated), then relative cue weights are gradually adjusted to reduce the misleading effect of the unreliable cue, consistent with previous perceptual studies of cue reweighting. The speed and flexibility of these two forms of learning provide an alternative explanation of why perception and action are sometimes found to be dissociated in experiments where some 3D shape cues are consistent with sensory feedback while others are faulty.

**NEW & NOTEWORTHY** When interacting with three-dimensional (3D) objects, sensory feedback is available that could improve future performance via supervised learning. Here we confirm that natural visuomotor interactions lead to sensorimotor adaptation and cue reweighting, two distinct learning processes uniquely suited to resolve errors caused by biased and noisy 3D shape cues. These findings explain why perception and action are often found to be dissociated in experiments where some cues are consistent with sensory feedback while others are faulty.

3D shape; cue combination; cue reweighting; motor learning; sensorimotor adaptation

## INTRODUCTION

Picking up a nearby object is a basic human behavior that involves a surprising level of computational complexity. To shape and orient the hand for a stable grasp, your visual system must first process a diverse assortment of three-dimensional (3D) shape cues and then combine these signals into a single estimate of the target object’s shape, which is then transformed into appropriate motor commands. Since the availability and quality of individual cues can vary widely from one situation to the next, leading to bias and noise in perception, the process of cue combination is one of the most challenging aspects of this problem. Indeed, even when viewing real, fully illuminated objects from within reaching distance, human visual perception often fails to provide veridical estimates of 3D shape (Heine 1900; Norman et al. 1996, 2000). This raises the question of how we manage to produce consistently accurate movements despite the variable distortions that afflict perception.

A popular explanation of this paradox is that perception and action are supported by separate visual processing of 3D shape information, with the purported “vision-for-action” system capable of recovering more accurate spatial estimates than the “vision-for-perception” system (Goodale and Milner 1992). One cornerstone of support for this theory is the literature regarding the effects of visual illusions on motor behavior, where many studies have reported that motor responses are more accurate than perceptual judgments of the same illusory stimuli. For example, Bruggeman et al. (2007) presented participants with the Ames window illusion, which is created by putting carefully constructed texture cues specifying a 3D scene in conflict with stereo cues specifying the actual scene, a flat surface. When participants were asked to make perceptual judgments regarding the degree of surface slant, they were misled by the biased texture cues. However, when asked to interact with the Ames window by making bimanual pointing movements targeting its left and right edges, the movements were, on average, more accurate with respect to the physical slant specified by the stereo cue. These findings were interpreted as evidence that motor planning relies preferentially on stereo information.

The Ames window is an example of an experimental stimulus that involves a biased slant cue: illusory texture information consistently indicates that the display is more slanted than it actually is. Meanwhile, other experiments have examined visuomotor responses in situations involving an unreliable cue,

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i.e., one that suddenly becomes less correlated with the physical layout of the environment. For example, Knill (2005) rendered slanted surfaces using conflicting stereo and texture information and asked participants to place an object so that its bottom would be parallel with the surface at contact. On some trials, one of the cues was perturbed to specify either more or less slant than the underlying physical surface. Therefore, unlike the study of Bruggeman et al. (2007), which involved a constant bias in the texture cue (and thus a relatively constant perceptual bias), the errors experienced in the study by Knill (2005) were variable, changing sign randomly throughout the task. Yet the results were similar: the average orientation of the handheld object when it made contact with the surface was slightly closer to the stereo slant.

Both of the cited studies, and others like them, have been interpreted as evidence that "vision-for-action" selectively relies on stereo information, enabling the motor system to avoid making mistakes based on faulty processing of other, typically less reliable cues (Goodale 2011). Stereo information is special, it is argued, because binocular disparities are a straightforward function of object shape, viewing distance, and interpupillary distance. Since interpupillary distance is relatively fixed in adults, an estimate of viewing distance from ocular convergence should be all the visual system needs to recover metric estimates of an object's 3D properties. Other cues, like texture, require the visual system to make additional, potentially complex assumptions (e.g., about the process that generated the texture pattern) before it is possible to arrive at any specific metric estimate.

This interpretation originates from the two visual streams theory, which has been broadly influential in perception and action research, explaining a variety of neuropsychological and psychophysical findings (Goodale 2011; Goodale and Milner 1992; Milner and Goodale 2008). Here, we focus specifically on testing an alternative explanation of the apparent preference for stereo information in visuomotor tasks involving biased and/or unreliable 3D shape cues. Our account eliminates the need to posit separate 3D shape estimates for perception and action, showing instead how some dissociations can be explained as artifacts produced by averaging over many trials where informative sensory feedback is available. We focus on the effects of two supervised learning processes, sensorimotor adaptation (Cesanek and Domini 2017) and cue reweighting (Atkins et al. 2001; Cesanek and Domini 2019; Ernst et al. 2000; Ho et al. 2009; van Beers et al. 2011; Welch 1978), that could shift motor responses in a way that appears to privilege stereo information (or potentially any other cue, depending on the feedback conditions). By accounting for these processes, we are able to show how averaged movement kinematics can appear to combine cues differently than perceptual judgments without positing separate cue-combination functions for perception and action.

### *Study Overview*

In *experiment 1*, we show that a standard computational model of sensorimotor adaptation can account for changes in the motor response during exposure to a constant bias in stereo information; this is the converse of the experimental design of Bruggeman et al. (2007), which involved a constant bias in texture information. In *experiment 2*, we examine how the motor response changes over time in the more complex scenario where one cue becomes uncorrelated with sensory feedback, producing variable errors. This is similar to the study of Knill (2005) and previous studies on cue reweighting in perception (Atkins et al. 2001; Ernst et al. 2000; Ho et al. 2009) and in action (Cesanek and Domini 2019; van Beers et al. 2011). Our results show that these two learning processes operate as expected in these situations, supporting our alternative explanation of why goal-directed actions appear to prefer stereo information in studies that provide stereo-consistent feedback. *Experiment 2* also serves to extend current knowledge of cue reweighting, a learning process that has been studied considerably less than sensorimotor adaptation. Whereas previous studies on cue reweighting in perception provided haptic information via tightly constrained exploratory hand movements and emphasized explicit intermodal comparisons of vision and touch, here we show that cue reweighting also occurs in a natural visuomotor task, extending the findings of two similar studies (Cesanek and Domini 2019; van Beers et al. 2011).

## METHODS

### *Participants*

Participants were between 18 and 35 yr old, right-handed and had normal or corrected-to-normal vision. They were either granted course credit or paid hourly as compensation. Informed consent was obtained from all participants before any participation. Our research protocol was approved by the Brown University Institutional Review Board (No. 0402991569) and performed in accordance with the ethical standards set forth in the Declaration of Helsinki. Fifteen participants were recruited for *experiment 1*. Forty-eight participants were recruited for *experiment 2*; 28 were assigned to the haptic-for-texture condition, and 20 were assigned to the haptic-for-stereo condition. One participant from the latter condition was excluded from analysis because more than half of their Grip Placement trials were marked for exclusion by the criteria indicated below.

### *Apparatus*

The experiment was run using a custom-built virtual reality apparatus (look ahead to Fig. 3*D* for an illustration). Participants sat with the chin resting 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 index finger and thumb nails, and the system was calibrated to track the tip of each distal phalanx. This motion-capture system was coupled to a virtual reality environment consisting of an oblique half-silvered mirror that reflected the stereoscopic image on a 19-in. CRT monitor to provide consistent accommodative and vergence information at the intended viewing distance (very small, probably negligible, discrepancies between accommodation and vergence would arise when fixating points with nonzero disparity). The room was completely dark, and an opaque back panel was placed on the mirror to prevent vision of the hand or of the physical surfaces providing haptic feedback. Participants viewed computer-generated 3D slanted surfaces with stereo and texture cues controlled independently via backprojection. Surface slants were obtained by rotating around a transverse axis through the middle of the object, which appeared at eye level at a distance of 40 cm. A frontoparallel surface (0° slant) diagonally subtended 13° of visual angle. The rendered 3D stimuli appeared to be floating in space beyond the mirror. Stereoscopic presentation was achieved with a frame interlacing technique in conjunction with liquid-crystal goggles synchronized to the frame rate. No visual feedback of the hand was provided. Haptic feedback was provided by a square plexiglass surface, attached to a stepper motor to control the slant and mounted on linear positioning stages to control the position. Precise alignment of the plexiglass surface with the rendered 3D stimuli was established at the start of each session. Before every trial, the positioning of the plexiglass surface was checked using additional Optotrak markers and corrected if necessary. A handful of familiarization trials were provided for both the Matching and Grip Placement tasks, using cue-consistent stimuli only.

### *Procedure*

*Experiment 1* involved two tasks. First, in the Matching task, participants matched the perceived slants of three stereo-texture conflict surfaces ($s_{T_i}$, $s_{S_i}$) with cue-consistent surfaces ($s_{match_i}$, $s_{match_i}$) where stereo and texture specified the same slant, such that $\Psi(s_{T_i}, s_{S_i}) = \Psi(s_{match_i}, s_{match_i})$, with the subscript $i$ indexing the three objects. The three cue-conflict stimuli were chosen such that, for each surface, stereo slant and texture slant differed by a constant conflict angle of 30°. Specifically, the stereo slants of the cue-conflict stimuli were 0°, 10°, and 20°, paired with texture slants of 30°, 40°, and 50° (look ahead to Fig. 3*B* for an illustration). On each trial, we allowed participants to switch freely between the fixed cue-conflict stimulus and an adjustable cue-consistent stimulus, using keypresses to make incremental changes to the slant of the cue-consistent stimulus until it appeared to match the slant of the cue-conflict stimulus. To prevent the use of motion information, we displayed a blank screen with a small fixation dot for an interstimulus interval of 750 ms whenever the stimulus was changed. Participants performed 5 repetitions of matching for each of the 3 fixed cue conflicts, for a total of 15 trials.

The resulting set of six stimuli (3 pairs of matched cue-conflict and cue-consistent surfaces) were then presented as stimuli in the Grip Placement task. With the hand shaped into a precision grip, participants reached toward the displayed surface with the goal of making the index finger and thumb hit the surface at the same time. At the starting position, the hand was held at approximately the same height as the surface, with the elbow on an armrest and the forearm pronated so the fingers pointed toward the surface. Participants were instructed to use only the wrist and arm to change the grip orientation while holding their fingers in fixed precision grip posture. This task is similar to handheld object placement tasks where cylinders are placed so that their bottoms are parallel with the surface at contact (Knill 2005), but it also engages the fingers' tactile sensitivity. A standard, three-phase "ABA" design was adopted for the visuomotor task. In the Baseline phase, participants reached toward their personalized set of cue-consistent surfaces for 30 trials. At the transition from Baseline to the Adaptation phase, the cue-consistent surfaces were suddenly replaced by the perceptually matched cue-conflict surfaces, with the underlying physical surface reinforcing the texture slant. Following 180 trials of exposure to these conflict surfaces, the experiment concluded with a 30-trial Washout phase, identical to Baseline. Throughout this task, we used a binned trial order such that each of the three surfaces was presented once before any one was repeated, facilitating local averaging of trials.

Participants in *experiment 2* also performed the Matching and Grip Placement tasks, but there were nine target stimuli presented during Adaptation (look ahead to Fig. 5*A* for illustration): three cue-consistent (main diagonal) and six cue-conflict (off-diagonal cells) stimuli. The six cue-conflict surfaces were perceptually matched with adjustable cue-consistent stimuli in the first block using the same psychometric procedure as *experiment 1*. We eliminated the Washout phase from this experiment to reduce the overall duration. During Baseline, the targets were nine cue-consistent stimuli: six personalized perceptual matches to the six cue-conflict stimuli from the target set, plus the three cue-consistent stimuli from the target set. These nine targets were presented four times each in a binned trial order for a total of 36 Baseline trials. During Adaptation, the visual stimuli were the nine target stimuli, and the physical surface slants were consistent either with the texture slants (haptic-for-texture group) or the stereo slants (haptic-for-stereo group). These were presented 14 times each in a binned trial order for a total of 126 trials.

### *Analysis*

Raw motion-capture position data were processed and analyzed offline using custom software. Missing frames due to marker dropout were linearly interpolated, and the 85-Hz raw data were smoothed with a 20-Hz low-pass filter. We excluded from analysis all trials where *1*) the proportion of missing frames exceeded 90%, *2*) fewer than five frames were not missing, *3*) the grip traveled $<$2.5 cm, or *4*) the markers were not visible during the final 5 cm of the movement. This combination of exclusion criteria was chosen because a valid precontact grip orientation could, in many cases, be extracted from trials with a high proportion of missing frames (see below for details). The final criterion, regarding visibility at the end of the movement, ensures that the extracted grip orientation is valid. Note that the average percentage of missing frames during the final 5 cm of movement was low: 8% in *experiment 1* and 2.5% in *experiment 2*. In *experiment 1*, these criteria resulted in the exclusion of 79 out of 3,600 trials. In *experiment 2*, these criteria resulted in the exclusion of 298 out of 7,776 trials.

In *experiments 1* and *2*, in-flight grip orientation was calculated as the declination of the projection of the line joining the fingertips onto the sagittal plane. From the grip orientation trajectory on each trial, we extracted the precontact grip orientation, a snapshot taken 10 mm before first contact (Fig. 1*A*). This was done to avoid any contamination caused by adjustments made after one of the fingers contacted the surface. To extract this kinematic landmark, we first processed the entire trajectory and then searched for the first motion-capture frame where either one of the fingers contacted the physical surface, defined as the frame with minimum orthogonal distance from each finger to the surface plane, and scanned 10 mm backward along the trajectory.

However, this precontact grip orientation does not represent the planned grip orientation because the movement is still in progress. For the data displayed in Fig. 4*C* (*experiment 1*), we used each participant's Baseline performance to determine how their measured precontact grip orientations related to the actual physical slants they intended to place the fingers on, presumably their "planned" grip orientations (Fig. 1*B*). As shown in Fig. 1, *B* and *C*, we fit a linear regression to this Baseline data and used the inverse of the estimated function to transform precontact grip orientations, our raw-dependent variable, into planned grip orientations. This does not affect the statistical analysis or the modeling of our data but helps to present the data in a more understandable format, with the dependent variable sharing the same metric as the rendered slant values.

In *Experiment 1*, we fit the error-correction parameter $b$ of our first adaptation model to minimize the root mean squared error of the model with respect to the average trial-by-trial grip orientations. To do so, we used the constrained optimization by linear approximation (COBYLA) algorithm (Powell 1998) of the nloptr package (Johnson, n.d.) in R (R Core Team 2014), constraining the fit so that $b$ was bound between 0 and 1. After fitting the model, we observed that participants' planned grip orientations converged on a slightly greater value than did the model, as the model was bound to converge on the actual physical slants that were presented. To incorporate this empirical measure of the fully adapted state into the model before making predictions for the Washout phase, we manually set the internal state of the model on the first trial of Washout to reflect the average change in grip orientations from Baseline to the final 30 trials of Adaptation.

The factorial design of the conflict stimuli in *experiment 2* allowed us to measure the relative influence of stereo and texture information in the Grip Placement task by estimating coefficients (slopes) for each cue via multiple linear regression according to *Eq. 5*, with the precontact grip orientation as the response variable. Unlike in *exper-*

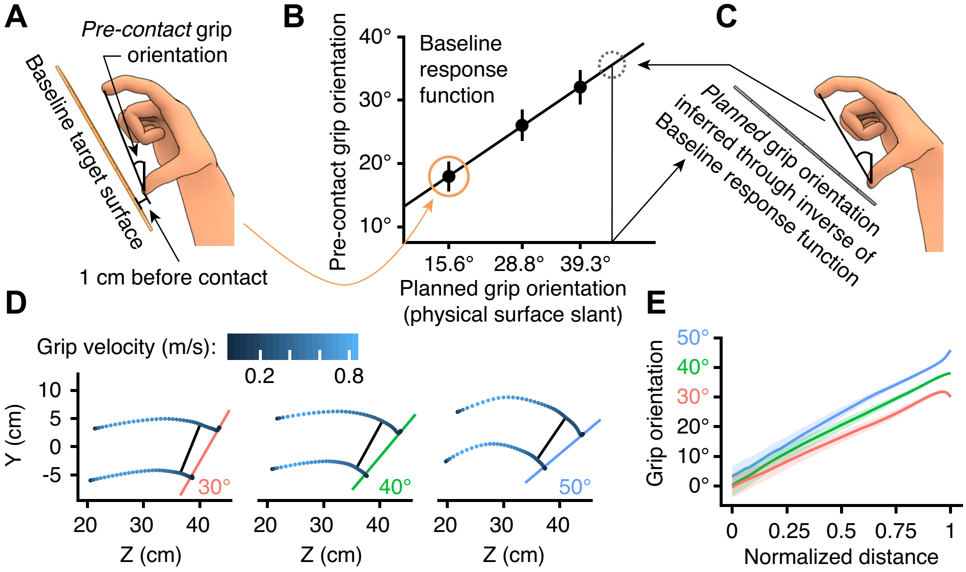

Fig. 1. Analysis of grip orientation. *A*: we extracted precontact grip orientations on each trial by first detecting the frame where first contact was made with the surface (by either finger) and then rewinding the spatial trajectory by 1 cm. *B*: the Baseline precontact grip orientations from *experiment 1*, plotted against the average cue-consistent surface slants they were aimed at, show a linear slope <1, like other common kinematic landmarks and their associated physical target properties, including the maximum grip aperture (MGA). *C*: for the analysis depicted in Fig. 4*C* (*experiment 1*), to obtain an estimate of the physical surface slant the participant expected (the "planned" grip orientation) from the measured precontact grip orientation, we inverted the linear function estimated using the Baseline cue-consistent data. *D*: sagittal view of representative fingertip position and velocity data from the Adaptation phase of *experiment 1* (upper: index finger; lower: thumb; connecting line: precontact grip orientation; colored line: physical surface). Origin is the cyclopean eye. *E*: average grip orientation profiles as a function of normalized movement distance (all trials of *experiment 1* Adaptation phase).

*iment 1*, we did not transform the precontact grip orientations into planned grip orientations: this was not necessary in *experiment 2* because we were interested only in how the slope coefficients from the multiple regression changed over time. Just as before, precontact grip orientations were measured by finding the moment at which one of the fingers first touches the surfaces and then scanning backward by 10 mm of hand movement. A regression was computed for each bin of nine trials within the Adaptation phase, producing a fine-grained timeline of the influence of each cue on precontact grip orientation. In Baseline, we computed the slope of the precontact grip orientation with respect to the perceptually matched slant values using simple linear regression in each bin.

In *experiment 2*, since there were no differences in procedure between the two feedback conditions until the Adaptation phase of the Grip Placement task, and since no significant differences were found in Matching performance between the two groups for any of the six cue-conflict stimuli, the two groups were combined when analyzing the Matching task. The two groups were also combined for the correlation analysis depicted in Fig. 6; additionally, in that analysis we excluded data from three participants whose grip orientations on the first Adaptation trial were extreme outliers (i.e., <10° or >55°).

## RESULTS

### *Experiment 1: Sensorimotor Adaptation Compensates for a Biased Slant Cue*

To motivate our model of sensorimotor adaptation to a biased slant cue, it will be helpful to walk through a short example of motor interaction with a cue-conflict stimulus akin to the Ames window. Consider the stereogram in Fig. 2*A*, which was constructed so that when cross fused, the perceived surface should appear to have a deeper slant than the flat plane of the document it is printed on (i.e., when held at about arm's length, the top edge should appear slightly beyond the page while the bottom edge is slightly protruding). As depicted in Fig. 2*B*, this perceived slant (yellow) is due to perceptual combination of a stereo slant (red) and a conflicting texture slant (blue) printed on the flat surface of the page (transparent frame). Now, imagine trying to simultaneously place your index finger on the top edge and your thumb on the bottom edge of this surface. If the perceived slant guides visuomotor planning, you will reach with your grip angled slightly forward, so the index finger leads the thumb. However, this means you will bump the physical page sooner than expected with your index finger (Fig. 2*C*), giving rise to an error signal. In the process of sensorimotor adaptation, this error signal is exploited to adjust the mapping from visually perceived slants to motor outputs so that the next movement will be more appropriate for the physical slant of the surface. As you repeatedly interact with this surface, error corrections accumulate, so after a few trials all of your reaches will tend to be accurate.

Sensorimotor adaptation to a constant bias in slant perception can be formalized using a linear state-space model of proportional error correction (Cheng and Sabes 2006; Thoroughman and Shadmehr 2000). On a given trial $n$, the observer perceives some slant $\hat{s}$ that is a function of the available texture and stereo information $\Psi(s_T, s_S)$:

$$\hat{s} = \Psi(s_T, s_S) \tag{1}$$

The planned grip orientation $y_n$ for that trial is the combination of the perceived slant $\hat{s}$ and an adjustable internal state $x_n$:

$$y_n = \hat{s} + x_n \tag{2}$$

When the planned grip orientation $y_n$ does not match the physical surface slant $s_\Phi$, haptic feedback produces an error signal $\varepsilon_n$ as a function of the difference between the planned grip orientation and the physical surface slant:

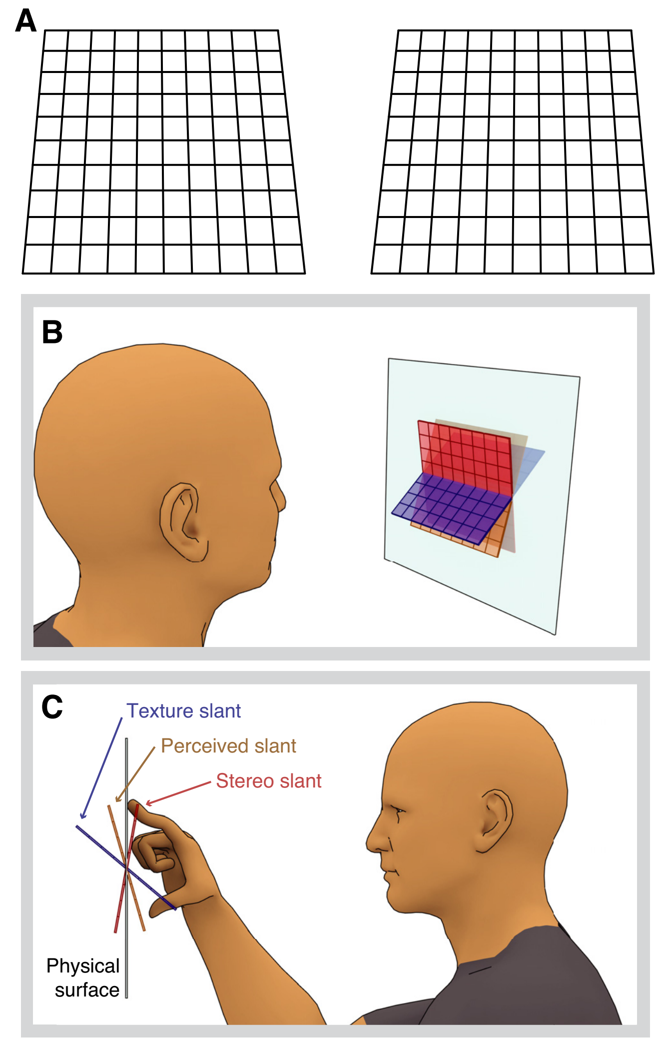

Fig. 2. Interacting with slanted surfaces defined by conflicting stereo and texture cues. *A*: example stimulus (cross fuse). Stereo information specifies a surface with the top edge nearer to the viewer than the bottom edge, while texture information specifies an opposite slant direction. Observers typically perceive a slant that is between the 2 component slants. *B*: an observer viewing the cue-conflict slant stimulus of *A*. The physical surface of the page is depicted by the large, transparent frame. The stereo and texture slants are shown in conflict, with the perceived slant in the middle. In this example of viewing a stereogram printed on a flat page, the physical surface does not match the perceived slant, stereo slant, or the texture slant. *C*: in our experiments, the observer attempts to place the index finger and thumb simultaneously on the displayed surface, as shown. When the planned grip orientation is not appropriate for the physical slant, an error signal is registered as one of the fingers bumps into the surface earlier than anticipated. We hypothesize that during this Grip Placement task the grip orientation will initially target the perceived slant but gradually come to target the haptically reinforced slant of the underlying physical surface. Unlike the example depicted here, the physical surfaces in our experiments were made to be consistent with either texture or stereo information, depending on the condition.

$$\varepsilon_n = f(y_n - s_\Phi) \approx y_n - s_\Phi \qquad (3)$$

Note that in *Eq. 3* we have opted to approximate the actual error signal by the difference between the planned grip orientation and the physical slant. This is not meant as a mechanistic claim that these two quantities are directly compared by the nervous system; in reality, this difference is simply the source of other error signals, such as discrepancies in the expected and actual timing or magnitude of contact forces (i.e., sensory-prediction errors; Säfström and Edin 2008). Having detected an error, the system updates the state of the visuomotor mapping for the next trial $x_{n+1}$ by extracting some of the error $\varepsilon_n$ according to the learning rate $b$:

$$x_{n+1} = x_n - b\varepsilon_n \qquad (4)$$

Therefore, with repeated reaches, error signals trigger cumulative adjustments to the visuomotor mapping, without necessarily modifying perception: planned grip orientations approach the physical slant while the slant percept remains stable. If the conflict between stereo and texture is removed, then reaches should still be biased by the now-adapted internal state and give rise to an aftereffect, often considered the hallmark of adaptation.

This model of sensorimotor adaptation to a biased slant cue can account for some dissociations between perceptual judgments and visually guided actions (e.g., Bruggeman et al. 2007) without supposing a fixed preference for stereo information in motor planning. Instead, the model maintains that motor planning relies on the same 3D shape estimates as perception but is additionally shaped by the contributions of an adjustable internal state. This idea was the focus of *experiment 1*, where we examined adaptation of the grip orientation during repeated Grip Placement (Fig. 2*C*) on three surface slants defined by texture and stereo cues, with haptic feedback that matched the texture cue but was consistently 30° deeper than the stereo cue (i.e., the stereo cue was biased).

*Experiment 1* tested two specific hypotheses: *1*) motor planning relies on perceived slant, without regard for the specific mixture of slant cues, and *2*) when perceived slant is biased by a faulty cue, the resulting movement errors cause proportional adjustments of the planned motor output on subsequent trials. To set up a straightforward test of the first hypothesis, we began the experiment with a perceptual Matching task, asking participants ($n = 15$) to produce two sets of stimuli that were perceived to have the same slants but were composed of different combinations of stereo and texture information. This was done by adjusting the slant of a cue-consistent stimulus ($s_T = s_S$; yellow line in Fig. 3, *A* and *B*) to match each of three fixed cue conflicts ($s_T = s_S + 30°$; blue and red lines indicating texture and stereo slants). These 3D perceptual matches are sometimes called slant metamers: objects perceived to have the same slant but with different combinations of the available slant cues (the name borrows from the psychophysical phenomenon of color metamerism, where different spectral distributions can elicit the same perceived color). Having obtained these perceptual matches, we predicted that equivalent motor responses would be produced when we suddenly switched from a cue-consistent stimulus to its matched cue conflict, or vice versa, in the Grip Placement task.

After the Matching task, participants completed the Grip Placement task, which followed a standard, three-phase adaptation design (Fig. 3*C*). Participants reached forward with a precision grip, controlling the grip orientation so that index finger and thumb would contact the surface simultaneously (Fig. 3*D*). In the Baseline phase (Fig. 3*C*, *left*), each participant interacted with the personalized set of cue-consistent stimuli they indicated during the Matching task. This phase emulated well-calibrated visuomotor coordination: the physical slant encountered at the end of each movement matched both cues. At the transition to the Adaptation phase (Fig. 3*C*, middle), the

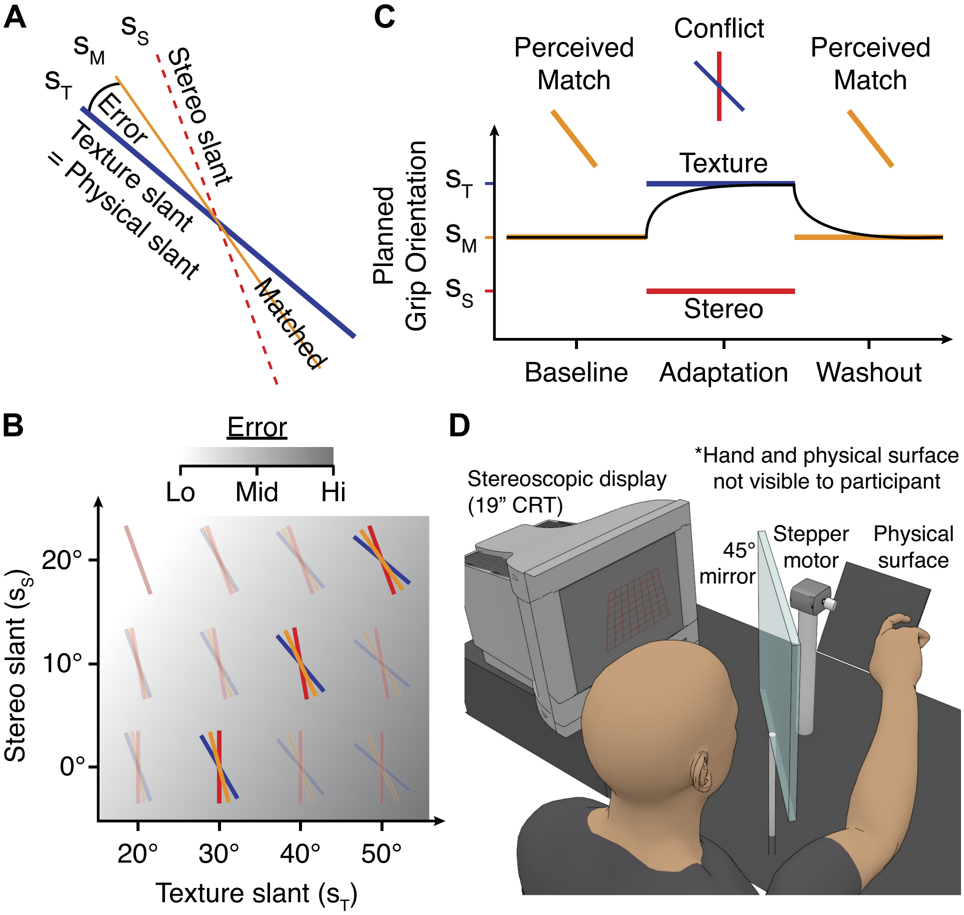

Fig. 3. *Experiment 1*: adaptation to a constant bias in stereo. *A*: a cue-conflict surface. Texture (blue) specifies the physical slant, while stereo (red) shows an underestimation bias; the perceived slant (yellow) is in between. Aiming at the perceived surface will produce a movement error. $s_T$, texture slant; $s_M$, matched slant; $s_S$, stereo slant. *B*: the 3 highlighted stimuli were used in *experiment 1*; the nonhighlighted combinations were not presented but are shown to provide context and to aid comparison with Fig. 5*A*. Stereo was consistently 30° shallower than texture slant, so errors were relatively constant (diagonal orientation of background gradient). *C*: timeline of Grip Placement task. In Baseline, cue-consistent surfaces (yellow) were presented to establish normal movement coordination (black trace). In Adaptation, cue-consistent surfaces were replaced by perceptually matched cue conflicts (blue/red). On the first trial of Adaptation, we predict the planned grip orientation (black trace) will be identical to Baseline, mirroring the perceptual equivalence of the stimuli. Planned grip orientations should then adapt toward the physical slants, which match the texture slants. At the transition to Washout, we switch back to cue-consistent surfaces, again predicting no sudden change in the motor response due to perceptual equivalence. Thereafter, we predict rapid convergence on Baseline performance. *D*: the multisensory virtual reality rig. The participant reaches with the right hand in a precision grip, orienting the hand to place index finger and thumb simultaneously on the observed surface, with haptic feedback from a physical surface aligned with the visual stimulus.

three cue-consistent stimuli were suddenly replaced by the three fixed cue conflicts (Fig. 3*B*). Here, we predicted that the grip orientation would not suddenly change because the stimuli were perceptually matched: notice how the black curve in Fig. 3*C* is at the same level as Baseline on the first Adaptation trial. In contrast, if the relative weight of stereo were greater in visuomotor than perceptual tasks, we would expect the motor response to shift downward on this first trial, following the change in stereo slant. Thereafter, the physical slants reinforced texture, so we predicted that the grip orientation would rapidly shift upward toward the texture slants. Finally, we switched back to the cue-consistent surfaces in a Washout phase (Fig. 3*C*, *right*); once again, we predicted no sudden change across the transition due to the perceptual matching, followed by rapid convergence on Baseline performance.

*Perceptual Matching task.* The results of the Matching task are presented in Fig. 4*A*, with mean cue-consistent slants of 15.6°, 28.8°, and 39.3° (yellow) for the three fixed cue conflicts ($s_S/s_T$ = 0°/30°, 10°/40°, and 20°/50°; red/blue). These data correspond to a relative weight on texture information $w_T$ of 0.60 (SE = 0.08), according to $s_{match} = w_T s_T + (1 - w_T) s_S$. We computed a relative weighting of texture and stereo information here, rather than a freely varying slope parameter, because the Matching task does not provide an estimate of absolute perceived slant; it only indicates the relative influences of the two conflicting cues (as discussed by Young et al. 1993). The relative weight of texture was relatively constant in the tested range, although there was a slight trend toward increased influence at greater slants, consistent with previous work (Hillis et al. 2004; Knill and Saunders 2003).

*Grip Placement task.* The results of the Grip Placement task are presented in Fig. 4, *B* and *C*. Figure 4*B* depicts the average planned grip orientations for each of the three cue-consistent match slants during Baseline (small circles), where the physical slants matched the perceived slants, as well as during the final 30 trials of Adaptation (large circles), after exposure to the perceptually matched cue conflicts where haptic feedback was deeper than the stereo slant but consistent with texture. We found that the planned grip orientations from the final 30 trials of Adaptation closely matched the physical slants, although on average slightly exceeding them.

Most importantly, the timeline of planned grip orientations depicted in Fig. 4*C* (averaged over the 3 targets) is highly consistent with our model of adaptation to a constant bias. At the transition from Baseline to Adaptation, where the stereo slant decreased considerably, the average grip orientation did not change ($P = 0.55$). If visuomotor behaviors were more sensitive to stereo information than perception, as posited the two-streams hypothesis, the grip orientation would have shifted to follow the change in stereo slant. To illustrate, suppose the perceptual weights were equal, $w_T = w_S = 0.5$. In this case, the switch from a cue-consistent slant of 25° to its perceptually matched cue conflict would involve increasing the texture slant and decreasing the stereo slant by the same amount, say ± 15°, yielding a texture slant of 40° and a stereo slant of 10°. Now, if we assume visuomotor weights that favor stereo, say $w_T = 0.25$ and

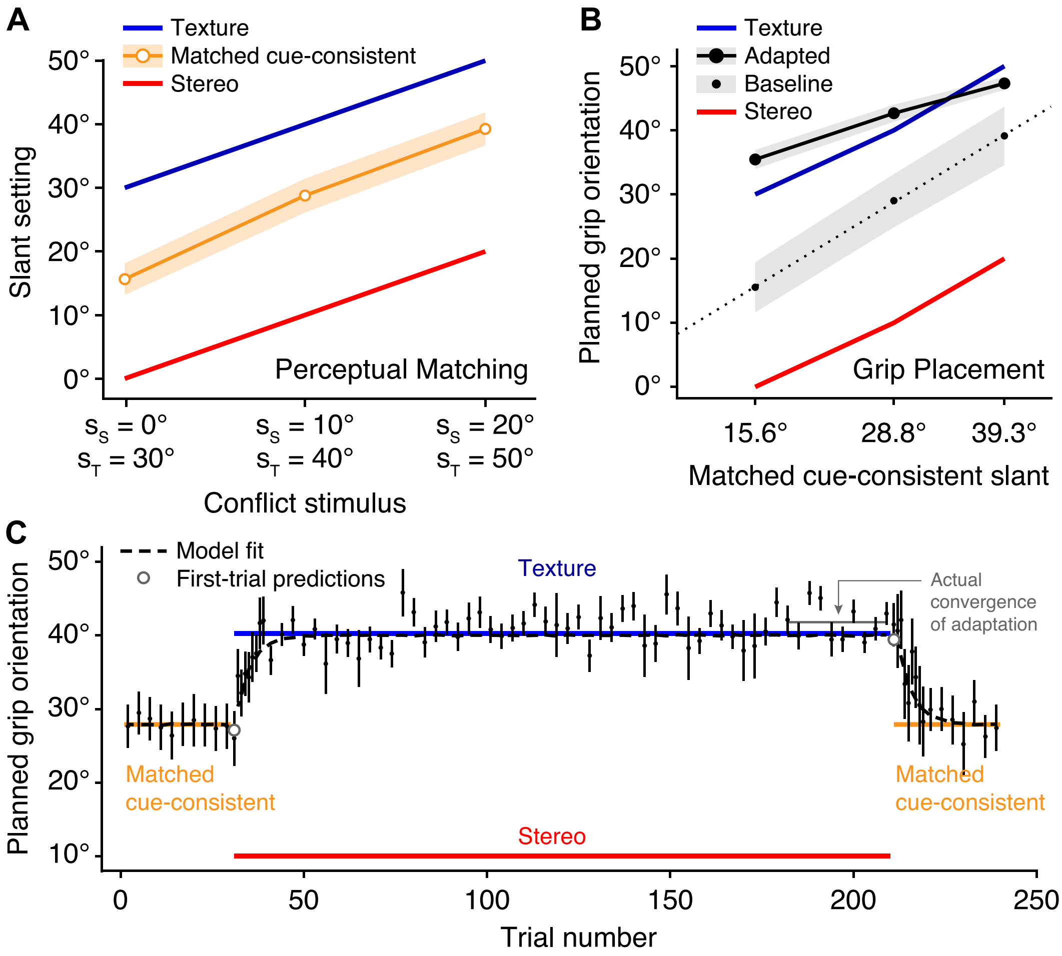

Fig. 4. *Experiment 1* results. *A*: Matching: cue-consistent slant settings (yellow) were between the component stereo (red) and texture (blue) slants of the cue-conflict stimuli. *B*: Grip Placement: Average grip orientations as a function of perceived slant, in Baseline and during the final 30 trials of Adaptation ("Adapted"). The dependent variable from *A* is plotted on the *x*-axis; this is why the solid red and blue lines (stereo and texture slants) are not straight. In Baseline, we assume the planned grip orientations were the physical slant values (see METHODS for details); this is why these data points (small points) fall on the (dotted) unity line. By the end of Adaptation (large points), planned grip orientations shifted toward the texture slants, which were reinforced by haptic feedback. *C*: Grip Placement: timeline of planned grip orientations, averaged over the 3 target surfaces. Our model accurately predicted the absence of any sudden change in grip orientation in the first trials of Adaptation and Washout (gray dots), and the time course of adaptation (dashed black line) was closely fit with an error-correction rate of 0.21. There was a slight underestimation of the actual convergence point of adaptation (compare model fit with gray line in *trials 181–210*; see also *B*, Texture vs. Adapted); we manually adjusted the internal state of the model on the first trial of Washout to account for this discrepancy.

$w_S = 0.75$, then this cue-conflict stimulus would produce a planned grip orientation of $40° \times 0.25 + 10° \times 0.75 = 17.5°$, closer to the stereo slant than to the perceived slant. Therefore, the lack of any change on the first trial of Adaptation is evidence of a common cue-combination function in perception and action. Following this initial trial, grip orientations rapidly shifted toward the reinforced texture slants. On the first trial of Washout, the planned grip orientation again matched the model prediction almost perfectly, with no sudden shift following the change in stereo slant. Thereafter, planned grip orientations converged back to their Baseline values in response to haptic feedback from the now-shallower physical slants. Model fitting to the complete time series estimated an error-correction parameter *b* of 0.21, indicating the rapid rate of learning achieved by sensorimotor adaptation.

### *Experiment 2: Cue Reweighting Reduces the Influence of an Unreliable Slant Cue*

*Experiment 1* shows that the visuomotor preference for stereo information reported in previous studies with a biased texture cue could be the result of averaging over a rapid sensorimotor adaptation process. However, this argument can only be applied to situations involving an approximately constant bias in the faulty cue, as sensorimotor adaptation is limited to uniform shifts of the motor output (assuming no anatomical, spatial, kinematic, or other features are available to consolidate adaptation within specific error contexts; Bingham et al. 2014; Donchin et al. 2003; Hwang et al. 2003; Pine et al. 1996; Taylor et al. 2011). Thus, for our account to be comprehensive, we must also explain how a preference for stereo information arises when other cues are unreliable, which leads to variable errors across a set of objects, as in the study of Knill (2005).

The adaptation process modeled in *experiment 1* assumes that adjustments of the motor output can only be applied on top of the combined 3D shape estimate $\hat{s} = \Psi(s_T, s_S)$. Yet previous work suggests it is possible to separately modify the influence of each cue before their perceptual combination, a process termed cue reweighting (Atkins et al. 2001; Cesanek and

Domini 2019; Ernst et al. 2000; Ho et al. 2009; van Beers et al. 2011). In the absence of sensory feedback, the relative weights of cues depend on a variety of factors, generally trading off in a way that favors cues with the greatest sensitivity to physical shape in the current viewing context (Coats et al. 2014; Hillis et al. 2004; Knill and Saunders 2003; Young et al. 1993). Here, however, we are concerned with gradual changes in cue weights that are driven by sensory feedback obtained during visuomotor interactions. To illustrate, consider a set of physical surfaces with varying slants. Both texture and stereo cues are available, but the texture cue is unexpectedly noisy, perhaps due to an irregular pattern of surface markings. Texture slant signals will therefore show a poor correlation with physical slant. As a result, visuomotor interactions with these surfaces will generate both positive and negative errors in haptic feedback, depending on whether this unreliable cue has indicated a spuriously large or spuriously small value. Since there is not a constant bias, sensorimotor adaptation (as modeled above) will fail due to interference between opposite error corrections. In contrast, cue reweighting changes the influence of each cue by adjusting cue-specific gains, making it well suited to reduce the variable errors arising from an unreliable cue. To capture this, we can rewrite the visuomotor mapping in *Eq. 2* as a linear function of the individual cues $s_T$ and $s_S$:

$$y_n = k_{T_n} s_T + k_{S_n} s_S + x_n \tag{5}$$

In this model, cue reweighting involves tuning the slope coefficients $k_{T_n}$ and $k_{S_n}$ to reduce the influence of unreliable cues and increase the influence of reliable ones. Note that because we have retained the intercept term $x_n$, this is a combined model that can capture both sensorimotor adaptation (according to *Eq. 4*) as well as cue reweighting (according to *Eq. 6*, below).

As a methodological aside, we acknowledge that when $y_n$ is a kinematic measure of the visuomotor response, as in our analysis, the slopes in *Eq. 5* capture not only the cue-combination process but the combined effects of multiple transformations: *1*) the transformation of the simulated slant values in the stimulus to single-cue slant estimates (the "single-cue mapping"), *2*) the transformation imposed by cue combination (the "cue weight"), and *3*) the transformation of the cue-combined slant estimate into the measured motor response (the sensitivity of the kinematic landmark). However, in an additive linear model, these transformations involve three independent slope terms that would simply multiply together, justifying our choice to estimate and present the slope coefficients in the compact form of *Eq. 5*.

To see how slope changes could arise through an error-based learning mechanism, consider the pattern of error signals that occurs across different values of an unreliable cue: spurious high values misleadingly increase the motor output, causing larger error signals, whereas spurious low values will decrease the motor output, causing smaller error signals. In other words, error signals will be positively correlated with the values of an unreliable cue. This fact can be exploited to perform slope adjustments with a simple rule for online supervised learning:

$$k_{S_{n+1}} = k_{S_n} - c\varepsilon_n s_S \tag{6}$$

where $c$ is a small, positive learning rate, $s_S$ is the input from a particular cue (in this case, subscript $S$ denotes stereo), and $k_{Sn}$ is the associated slope parameter on trial $n$. Through simulation, it can be shown that this learning rule is most robust when paired with rapid adjustments that compensate for constant errors, as modeled in *experiment 1*. When constant error is removed, variable errors due to the unreliable cue will be centered on zero, such that spurious small values of this cue cause negative errors, yielding a small negative product in the second term (before the subtraction), and spurious large values of this cue cause positive errors, yielding a large positive product in the second term. Therefore, if errors are centered, on average the second term will be positive for an unreliable cue and the associated slope will be gradually reduced. Notice that under a positive constant error, the product in the second term yields even larger positive values for an unreliable cue. Although this might seem desirable because it would more rapidly reduce the influence of this cue, positive constant error actually produces inappropriate reductions in the slopes associated with all available cues, including those that are most reliable. Negative constant error, on the other hand, initially causes the influence of the unreliable cue to increase, until even more dramatic increases in the slopes associated with reliable cues cause the unreliable cue's slope to be driven back down. In sum, the unstable behavior of this learning rule under constant error suggests a sensible complementarity with the simultaneous process of sensorimotor adaptation. Intriguingly, these observations also show why this learning rule predicts that interfering error signals are necessary to elicit cue reweighting, consistent with our previous findings on this topic (Cesanek and Domini 2019).

To examine cue reweighting in a natural visuomotor task, in *experiment 2* we asked participants to interact with a set of stimuli where one cue is uncorrelated with haptic feedback. The target stimuli were nine different surfaces rendered with independently varying stereo and texture slants ($s_T \in \{15°, 30°, 45°\} \times s_S \in \{15°, 30°, 45°\}$), in either a haptic-for-texture condition ($n = 28$) or a haptic-for-stereo condition ($n = 20$). Figure 5*A* illustrates the stimulus set: the three stimuli located along the identity line are cue-consistent slants, whereas the other six stimuli (off-diagonal in Fig. 5*A*) are rendered with different degrees of cue conflict. Critically, stimuli on the opposite sides of the identity line bias perception in opposite directions with respect to haptic feedback, leading to conflicting error signals from one trial to the next. In this stimulus set, since the faulty cue is completely uncorrelated with haptic feedback, the optimal solution is to eliminate that cue's influence and to increase the influence of the reinforced cue to match Baseline performance.

*Perceptual Matching task.* As in *experiment 1*, participants first performed a perceptual Matching task, indicating the cue-consistent slant that appeared to match each cue conflict in the uncorrelated stimulus set. The perceptually matched cue-consistent slants were set, on average, about halfway between the component stereo and texture slants of the six cue-conflict stimuli (Fig. 5*B*). These data correspond to a texture weight of 0.56 (SE = 0.04), similar to the relative weight on texture information of 0.60 found in *experiment 1*.

*Grip Placement task.* Following the Matching task, participants performed the Grip Placement task. The slope coefficients estimated in each bin of this task are depicted in Fig. 5*C* (haptic-for-texture group) and Fig. 5*D* (haptic-for-stereo group). During the Baseline phase, terminal grip orientations

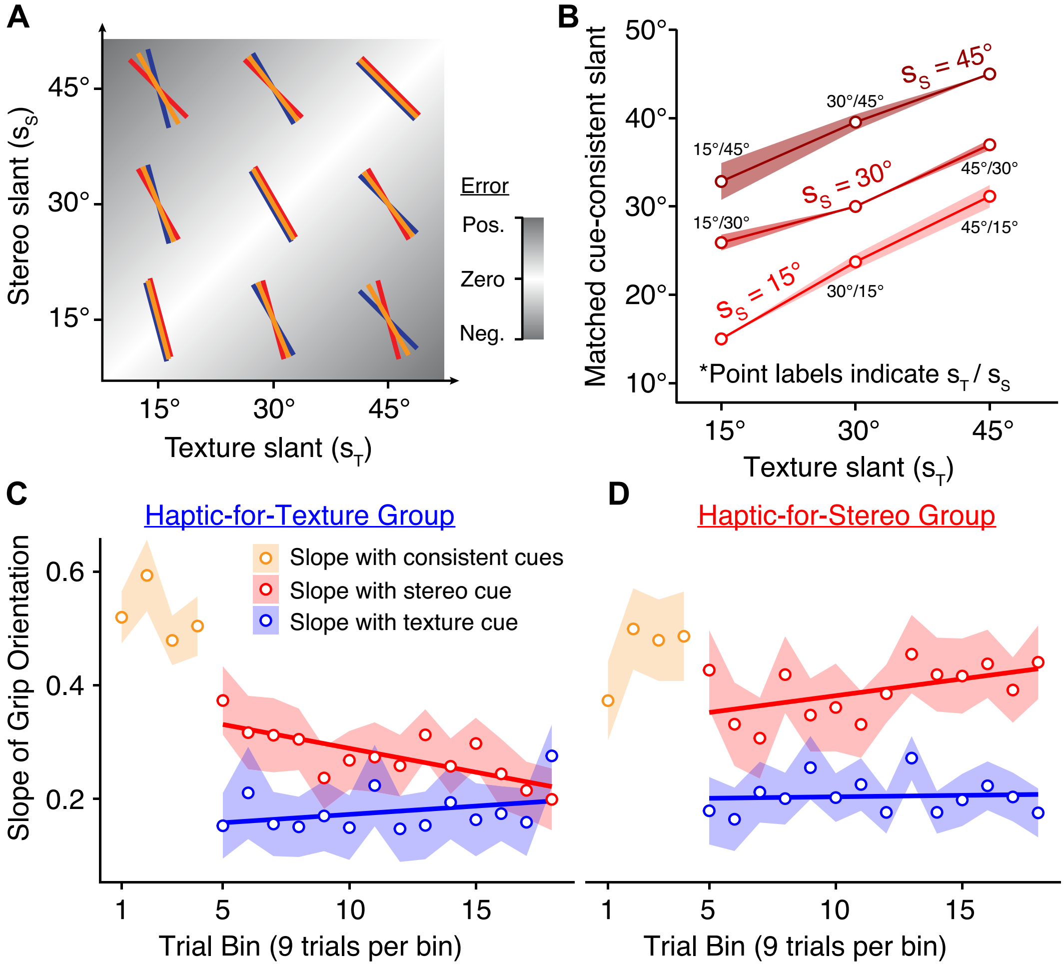

Fig. 5. *Experiment 2*: uncorrelated stimulus set and results. *A*: 9 surfaces obtained by combining 3 texture slants (blue) and 3 stereo slants (red). Main diagonal contains 3 cue-consistent slants; the 6 off-diagonals are cue conflicts. For half of the cue conflicts (*bottom right*), the expected cue-consistent match (yellow) is shallower than texture and deeper than stereo and vice versa for the other half (*top left*). As a result, when haptic feedback reinforces 1 cue, conflicting positive and negative movement errors should be experienced. To reduce these errors, cue reweighting is required. *B*: matching results for the 9 target stimuli. Texture slant is indicated on the *x*-axis, and stereo slant is indicated by the groupings (different shades of red). Perceptually matched cue-consistent slants (*y*-axis) were midway between the 2 component values of the 6 cue conflicts. *C* and *D*: Grip Placement results: in each bin, participants aimed at each stimulus once. In Baseline, we regressed grip orientations against the cue-consistent match slants (yellow). In Adaptation, we presented the 9 target stimuli with physical slant reinforcing texture (*C*) or stereo (*D*). Stereo (red) and texture (blue) slopes estimated via multiple linear regression. Solid lines depict linear regression on these slopes as a function of bin number.

were related to cue-consistent slants by a slope of 0.50 (SE = 0.03; yellow points), comparable to the slope of 0.60 found in the Baseline phase of *experiment 1*. In the Adaptation phase, we obtained independent slopes for stereo (red points) and texture (blue points) in each bin via multiple linear regression; these indicate the sensitivity of the precontact grip orientation to each cue. In the first bin of Adaption, these slopes sum to 0.56 (SE = 0.05), not significantly different than the mean slope observed in Baseline ($P$ = 0.17), demonstrating that the overall sensitivity of the motor response remained the same when we changed the stimuli. Neither the Baseline slope nor the summed slopes in the first bin of Adaptation differed significantly between feedback conditions. To measure changes in the cue slopes over time, we fit additional linear regressions as a function of Adaptation bin number (solid red and blue lines). The slope coefficients obtained from these regressions indicate the bin-wise rate of change in the sensitivity of the motor response to each cue. Analyzing this rate-of-change measure using a mixed-design ANOVA (Feedback Group × Slant Cue), we found a significant interaction [$F(1,45) = 5.13$, $P = 0.028$], confirming that the two feedback conditions elicited opposite changes in the relative influences of stereo and texture.

Follow-up analyses revealed a significant difference between feedback conditions in the rate of change of the stereo slope [one-tailed, two-sample $t$ test; $t(39.79) = 3.47$, $P$ = 3.2e-4], but not in the rate of change of the texture slope [$t(44.06) = 0.44$, $P = 0.33$]. Additional tests demonstrated that changes in the stereo slope were observed in both conditions, significantly decreasing in the haptic-for-texture condition [mean = −0.0084 per bin, $t(27) = 3.09$, $P$ = 0.0023] and significantly increasing in the haptic-for-stereo condition [one-tailed $t$ test; mean = +0.0059 per bin, $t(18) = 1.86$, $P$ = 0.040]. However, it is clear from Fig. 5, *C* and *D*, that the observed changes fell short of the optimal form of cue reweighting that might have been achieved. Ideally, sensitivity to the reliable cue should have increased to match (or even slightly exceed) Baseline sensitivity to cue-consistent stimuli, while sensitivity to the unreliable cue should have dropped to zero. Further research is needed to identify the constraints that produced this suboptimal cue reweighting.

Additionally, similar to *experiment 1*, we found evidence that on the first trial of Adaptation (i.e., the first interaction with a cue-conflict object), participants' precontact grip orientations were well predicted by their final Baseline interaction with the perceptually matched cue-consistent object [Fig. 6; Pearson's 0.67, $t(42) = 5.82$, $P = 7.2e\text{-}7$]. Critically, we also found that the changes in grip orientation from Baseline to first Adaptation trial (i.e., the residuals from the black dashed unity line in Fig. 6) are not significantly correlated with the change in stereo slant [Pearson's $r = 0.26$, $t(42) = 1.77$, $P = 0.084$]. This first-trial analysis is consistent with our demonstration in *experiment 1* that, before giving informative sensory feedback, perceptually matched slants with different combinations of stereo and texture information are treated as equivalent by the visuomotor system.

To summarize, we found that the sensitivity of the terminal grip orientation to stereo information was enhanced over time when stereo was reliably correlated with physical surface slant and reduced over time when it was uncorrelated with physical slant. Meanwhile, the sensitivity to texture information remained relatively constant throughout Adaptation, regardless of the feedback condition. However, to avoid improper interpretation of these findings, it is important to recall our discussion of *Eq. 5*, considering that multiple processes contribute to the compact slope estimates presented here. In particular, we cannot infer from these results that the influence of stereo increased while the influence of texture stayed the same. For example, in the haptic-for-texture condition (Fig. 5*C*), it is entirely possible that the weight of texture information in the cue-combination process increased over time, but this was masked in our data by a simultaneous reduction in the sensitivity of our kinematic measurement to changes in the cue-combined slant estimate. Such a regression toward the mean physical slant is certainly suggested by the decrease in the sum of the two slopes. Yet it is equally plausible that our observations of so-called "reweighting" are actually changes in processing of individual cues, occurring upstream of the cue-combination process (see Discussion of *experiments 2* and *3* in Atkins et al. 2003). Both possibilities are fully consistent with existing findings on cue reweighting. For the present argument, however, the critical observation from *experiment 2* is that the relative influences of stereo and texture information shifted over time to favor the reinforced cue. The data therefore support our main claim that estimates of relative cue weights can be modified in a single session of a natural, goal-directed visuomotor task, causing them to differ from those measured in separate perceptual tasks.

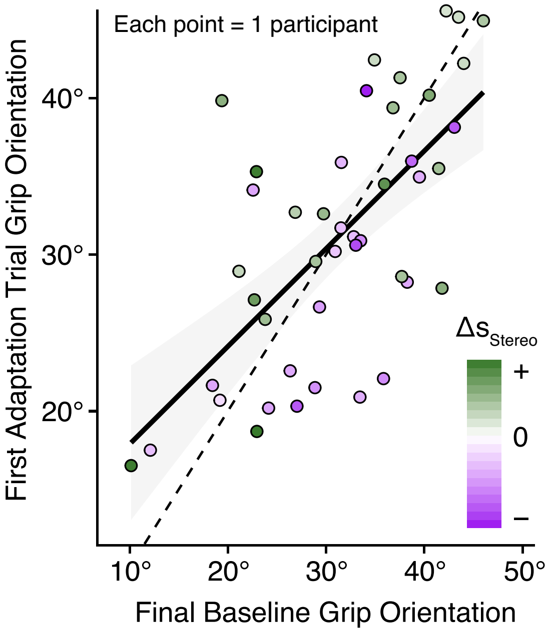

Fig. 6. *Experiment 2*: grip orientations for perceptually matched objects at the end of Baseline and on the first trial of Adaptation. Across participants, the grip orientation on the first trial of Adaptation (the very first presentation of a cue-conflict slant) was strongly predicted by the grip orientation of the final Baseline reach toward the corresponding matched cue-consistent slant. In contrast, the change in grip orientation at this transition (residual of each point from the dashed unity line) was not significantly correlated with the change in stereo slant from the cue-consistent slant to its perceptually matched cue-conflict slant ($\Delta s_{Stereo}$ coded by the color gradient).

## DISCUSSION

In two experiments, we asked participants to repeatedly reach toward 3D slanted surfaces defined by different combinations of stereo and texture information, controlling their grip orientation so that the index finger and thumb contacted the surface simultaneously. One of the available slant cues was rendered to be consistent with the haptic feedback received at the end of the movement, while the other cue was rendered either with a constant bias (*experiment 1*) or with noise (*experiment 2*) with respect to the haptic feedback. Our results demonstrate that the movement errors experienced during these tasks led to sensorimotor adaptation and cue reweighting, two different types of supervised learning that are uniquely appropriate for reducing the deleterious effects of biased and noisy slant cues, respectively. Notably, each of these types of distortion has been used in past experiments that aimed to test whether perceptual and visuomotor responses are mediated by separate cue-combination functions. The present experiments demonstrate that these short-term learning processes are active during natural goal-directed visuomotor behavior and that when they are properly accounted for, the relative influences of stereo and texture information in perception are the same as in action, as indicated by our first-trial analyses.

Both experiments yielded evidence that movement planning relies on the same cue-combined estimates of 3D shape as perceptual judgments, in contrast to previous claims that visuomotor tasks activate a separate cue-combination mechanism with a hardwired preference for stereo. We were able to demonstrate this only by carefully determining different combinations of stereo and texture information that were perceived to have the same slant and suddenly switching between these slant metamers in an ongoing visuomotor task. This precise technique was especially necessary in *experiment 1* because of how rapidly sensorimotor adaptation occurs. Indeed, we observed that sensorimotor adaptation operates as expected when an available slant cue becomes biased, in line with the standard proportional error-correction model. The model-estimated error correction rate of 0.21 from *experiment 1* indicates a fast exponential time course, likely reflecting the combined contributions of implicit and explicit components of adaptation (Taylor and Ivry 2011; Taylor et al. 2014). These results support the argument that some perception-action dissociations arise because sensory feedback drives the motor response toward cues that are more physically accurate, even when the 3D shape estimate used for motor planning remains biased.

Whereas sensorimotor adaptation is well-suited for situations involving constant biases, cue reweighting is required when the signals from one 3D shape cue have become less correlated with physical shape. Consistent with previous perceptual studies (Atkins et al. 2001; Ernst et al. 2000; Ho et al. 2009), *experiment 2* showed that exposure to an unreliable slant cue produces cue reweighting in the planned grip orientation. Unlike earlier studies on this topic, we did not measure perceptual changes, focusing solely on the visuomotor response to test two predictions: *1*) that before receiving informative sensory feedback, perceptually equivalent stimuli rendered with different combinations of stereo and texture information (i.e., slant metamers) would be treated equivalently in motor planning, and *2*) that a brief session of repeated interactions would change the relative cue weights measured from the visuomotor response. We found support for each of these predictions, thus showing that dissociated cue weights measured in separate perceptual and visuomotor tasks do not necessarily imply two independent cue-combination processes.

Although it does not affect our main conclusion, we should note that the absence of a perceptual posttest in *experiment 2* leaves open the possibility that visuomotor cue reweighting occurred without accompanying changes in perception. Thus, while our data from the first trial of the Adaptation phase in both experiments strongly suggest that motor planning is based on the same slant estimate as perception, we cannot definitively rule out the possibility that the visuomotor system can make further adjustments to relative cue weights that are independent of perception, perhaps by additional filtering of the input signal received from perceptual processing. Regardless, the present data do not support the strong form of the two-visual streams hypothesis, in which the visuomotor system is said to have a hardwired preference for stereo information, with a cue-combination function that is fully independent of perception.

Another feature of the present results that should be investigated further is why cue reweighting occurs so slowly, a finding mirrored by our other recent study on grasping (Cesanek and Domini 2019). One answer is suggested by the learning rule of *Eq. 6*: if movement error signals are used to update weights after each targeted movement, the learning rate must be extremely low to avoid instability. By making small adjustments that gradually accumulate, the system ensures that it is responding to a consistent, systematic pattern in the error signals that is directly related to cue reliability. Another possible explanation is related to the natural variability in cue reliabilities. These presumably do not fluctuate dramatically in the short term under natural conditions, possibly causing the system to become rather inflexibly tuned to the relative weightings appropriate for typical human environments. In any case, it is notable that measurable changes occurred at all within our ~15-min training, a briefer exposure period than any previous study on cue reweighting.

With respect to the mechanism of cue reweighting, we have found in another study that cue reweighting of the motor response does not occur during exposure to constant biases but only in response to reduced correlation of one available cue with haptic feedback (Cesanek and Domini 2019). An important remaining question is why altered correlations between individual cues and haptic feedback are necessary to produce cue reweighting. At present, most researchers approach the phenomenon of cue reweighting from the perspective of Bayesian cue combination (cf. Knill and Saunders 2003; Maloney and Landy 1989; Young et al. 1993): statistically, the optimal way to combine multiple unbiased but noisy estimates of the same world property is to assign linear weights to the single-cue estimators based on their relative reliabilities (hence the name cue reweighting; Atkins et al. 2001; Ernst et al. 2000; Ho et al. 2009). From this perspective, it is natural to hypothesize that the mechanism supporting cue reweighting involves a direct estimate of the reliability of each cue. One way to coarsely estimate the relative reliabilities would be to monitor their correlations with haptic feedback over the course of repeated interactions. Although they will be noisy, these correlations could theoretically serve as proxies for the actual cue reliabilities, and cue weights could be set accordingly. In *Eq. 6*, we have suggested an alternative that might be viewed as an approximation to this normative statistical principle. However, it does not require the system to maintain a direct estimate of cue reliability by computing correlations over multiple observations. Instead, under this learning rule it is possible to leverage movement-related error signals to update cue weights on a trial-by-trial basis. Additionally, this novel formulation helps to draw a potential connection between the processes of sensorimotor adaptation and cue reweighting.

Finally, we should directly address a few potential criticisms of our conclusions. Concerning our visuomotor task, one might object that the two visual streams literature has focused primarily on grasping movements aimed at small objects, involving size estimates, whereas we studied a finger placement task that primarily involves slant estimates. Recall, however, that our finger placement task closely emulates the object placement task of Knill (2005), discussed in the INTRODUCTION. In that study, stereo cues appeared to be weighted more heavily in action than in perception, and this finding has since been cited as evidence of dissociated cue-combination functions (e.g., Goodale 2011, p. 1570). Nonetheless, one might still choose to disregard placement tasks altogether, arguing that these should not be expected to show a different cue-combination function than perception. However, in a follow-up study where participants reached-to-grasp 3D objects from front-to-back, we found similar evidence of a single cue-combination function (see Fig. 3*B* of Cesanek and Domini 2019), suggesting that this result is not task specific. At the same time, it is important to recognize the issue of task specificity is potentially complex and might not be fully resolved without extensive experimentation under a variety of task conditions. The present results do not rule out the possibility of specific task contexts in which perception of a target object incorporates more (or less, or a different combination) of the available visual information than a concurrent motor plan.

A second potential criticism is that the presentation of only three different slants during each phase of *experiment 1* affords the possibility of storing the required grip orientations in a look-up table, whereas our model assumes the use of a linear mapping from perceived slant to planned grip orientation. Note, however, that at the critical transitions in *experiment 1*, although the perceived slants were matched, the general appearance of the stimuli changed, such that they would be discriminable side-by-side. Therefore, a look-up table learned for the Baseline cue-consistent stimuli would not contain a relevant entry for the newly introduced cue-conflict stimuli. Therefore, learning the individual stimuli fails to explain how responses were generated at these changepoints, while our model closely captures the observed behavior.

Lastly, one might question our generic assumption that slant estimates were, in fact, the inputs to motor planning in our visuomotor task. In contrast to this assumption, Smeets and Brenner (1999) and Smeets et al. (2019) have defended an elegant alternative model of precision-grip control in which thumb and index finger movements are planned as two independent pointing movements aimed at two separate egocentric locations. Notably, their model provides another plausible explanation of the apparent stereo preference in visuomotor tasks involving 3D stimuli. According to their model, the visuomotor interactions in these studies are guided by egocentric distance estimates, which tend to rely strongly on oculomotor vergence information from recent fixations (which would be consistent with stereo) and to be relatively insensitive to texture patterns and other pictorial information. In our experiments, however, we found that perceptually matched stimuli with different values of stereo slant elicited identical motor responses before sensory feedback (Figs. 4 and 6). Thus we can conclude either *1*) that our perceptual judgments were also based on egocentric distance estimates from multiple surface locations or *2*) that 3D property estimates were in fact used for movement planning in our tasks. As a result, our main conclusions are unchanged under the double-pointing model of precision-grip control.

In summary, we have shown that the operation of sensorimotor adaptation and cue reweighting over very short timescales can account for the preferential reliance on stereo information in visuomotor tasks compared with perceptual tasks. Additionally, before receiving informative sensory feedback, perceptually matched slant metamers elicited indistinguishable visuomotor responses despite having different combinations of stereo and texture slant. In contrast to the dissociated view of perception and action, these results suggest a link between these two functions: distortions of 3D shape perception will lead to improperly planned movements, but the resulting sensory feedback signals enable the system to rapidly compensate for those upstream distortions.

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## DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

## AUTHOR CONTRIBUTIONS

E.C. and F.D. conceived and designed research; E.C. performed experiments; E.C. analyzed data; E.C., J.A.T., and F.D. interpreted results of experiments; E.C. prepared figures; E.C. drafted manuscript; E.C., J.A.T., and F.D. edited and revised manuscript; E.C., J.A.T., and F.D. approved final version of manuscript.

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