MST Responses to Pursuit Across Optic Flow With Motion Parallax

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Upadhyay, Urmen D., William K. Page, and Charles J. Duffy. MST responses to pursuit across optic flow with motion parallax. J Neurophysiol 84: 818–826, 2000. Self-movement creates the patterned visual motion of optic flow with a focus of expansion (FOE) that indicates heading direction. During pursuit eye movements, depth cues create a retinal flow field that contains multiple FOEs, potentially complicating heading perception. Paradoxically, human heading perception during pursuit is improved by depth cues. We have studied medial superior temporal (MST) neurons to see whether their heading selectivity is also improved under these conditions. The responses of 134 MST neurons were recorded during the presentation of optic flow stimuli containing one or three speed-defined depth planes. During pursuit, multiple depth-plane stimuli evoked larger responses (71% of neurons) and stronger heading selectivity (70% of neurons). Responses to the three speed-defined depth-planes presented separately showed that most neurons (54%) preferred one of the planes. Responses to multiple depth-plane stimuli were larger than the averaged responses to the three component planes, suggesting enhancing interactions between depth-planes. Thus speed preferences create selective responses to one of many depth-planes in the retinal flow field. The presence of multiple depth-planes enhances those responses. These properties might improve heading perception during pursuit and contribute to relative depth perception.

INTRODUCTION

Optic flow contains a focus of expansion (FOE) that indicates heading direction during self-movement (Gibson 1950). Concurrent pursuit eye movements add rotation to the retinal image that causes the FOE to be displaced from the heading. During pursuit, depth cues from objects at different distances from the observer can create multiple retinal flow patterns that eliminate the singular FOE (Longuet-Higgins and Prazdny 1980).

Nevertheless, human observers show improved heading perception when depth is added to optic flow during pursuit (Royden et al. 1992; Stone and Perrone 1997; Warren and Hannon 1990). This might suggest that heading perception does not always rely on FOE identification and that other mechanisms might dominate during pursuit. Feature extraction, template-matching, and probabilistic network models have been shown to be viable possibilities (Koenderink 1986; Lappe and Rauschecker 1993; Perrone 1992), but there is no consensus regarding which model is best.

Neurons in the medial superior temporal area (MST) of monkey extrastriate visual cortex respond to optic flow (Saito et al. 1986). Many show heading selectivity (Duffy and Wurtz 1991b, 1995; Graziano et al. 1994; Orban et al. 1992; Tanaka et al. 1989) that persists during pursuit across optic flow that does not have depth cues (Bradley et al. 1996; Page and Duffy 1999).

We studied MST neuronal responses to optic flow with depth-plane stimuli. As with human observers, depth-planes enhance responses to neuronal optic flow during pursuit. A brief report of this work has appeared previously (Upadhyay et al. 1998).

METHODS

Animal surgery and training

Single neurons were recorded from two cerebral hemispheres of two rhesus monkeys. Surgery was performed under general anesthesia using inhaled Isoflurane. Bilateral scleral search coils (Judge et al. 1980), a head holder, and bilateral recording cylinders were surgically implanted. The recording cylinders were placed over 1-cm trephine holes above area MST (AP –2 mm, ML ±15 mm, angle 0) and encased in a dental acrylic cap. Postoperative analgesia was administered as judged appropriate by veterinary staff. All protocols were approved by the University Committee on Animal Research and complied with Public Health Service Policy on laboratory animals.

The monkeys were trained to sit in a primate chair and perform a visual fixation task that was monitored with magnetic search coils (Robinson 1963). Trials began with a red fixation point (0.25° diam, 2.7 cd/m²) centered on a rear-projection tangent screen 48 cm from the monkey. The monkey fixated within 500 ms and maintained fixation (±3°) for the 1-s stimulus period and an additional variable period (0.5–1.5 s) after the stimulus. Successful trials ended with a tone and a liquid reward.

Pursuit stimuli

In pursuit eye movement trials, the monkey followed a red light-emitting diode fixation target reflected off a two-axis mirror-galvanometer system. Each trial began with target fixation at the center of the screen. The target was then extinguished and re-appeared at an eccentricity of 7.5° along the horizontal or vertical axis. The target then moved at 15 frames/s across the center of the screen. Stimulus illumination began 66 ms after the onset of target movement and continued for 1 s while the monkey stayed within a 3° window. The stationary FOE maintained a constant position on the screen to provide a constant simulated heading direction in body-centered coordinates (Fig. 1A).

A 76° × 76° viewing aperture moved with the pursuit target across...
the $91° \times 91°$ optic flow stimulus to ensure a constant area of retinal stimulation. The stimulus first appeared with the viewing aperture shifted by $7.5°$ so that its peripheral edge was $46°$ from the center of the screen. The viewing aperture then moved with the pursuit target at $15°/s$ to its final position $31°$ from the center. The FOE remained at the screen location specified for that optic flow stimulus. The moving frame was not seen as an additional environmental surface by human observers, presumably because it moved with the eyes.

**Visual stimuli**

The optic flow stimuli consisted of 500 white dots ($0.19°$ at $2.61$ cd/m$^2$) on a black background ($0.18$ cd/m$^2$) in a $480 \times 480$ pixelation of the central $91° \times 91°$ of the visual field. A pseudorandom sequence of visual stimuli were presented by a 486-based personal computer driving a television projector (Electrohome ECP4100) at a frame rate of $60$ Hz. The stimuli covered a $76° \times 76°$ area centered in the visual field during fixation trials and passing through the central visual field in pursuit trials.

Dot motion in the optic flow stimuli simulated the observer’s approach to a remote fronto-parallel single- or triple-plane surface as an outward radial pattern of dots emanating from its FOE. During simulated forward self-movement the observer moved at $0.5$ m/s toward a single depth plane at $0.5$ m or toward three depth planes at $0.38$, $0.5$, and $0.63$ m distance. The dots in each plane were evenly distributed in a random pattern in the first frame and were assigned a random lifetime of $1–60$ frames. Dots were replaced at expiration or by a smoothing algorithm to maintain a uniform dot density across all frames in all stimuli.

Nine optic flow stimuli were used that contained FOEs at the center of the screen or at one of eight positions, displaced $30°$ from the center, and distributed at $45°$ intervals around $360°$ (Fig. 1B). Two stimulus sets were presented containing either three superimposed speed-defined depth planes with 166 dots in each speed plane (Fig. 1C), or a single speed plane with 500 dots (Fig. 1D). Dots accelerated as a sine $\times$ cosine function of their distance from the FOE maintaining an average speed of $40°/s$ for the single-plane, and $20$, $40$, and $60°/s$ for the triple-plane stimuli. Finally, the individual speed-defined planes were presented to test the speed sensitivity of the neurons. All of these stimuli were presented in a fully interleaved design.

**Neuron recording**

Epoxy-coated tungsten microelectrodes (Microprobe) were passed through a transdural guide tube positioned within the recording cylinder (Crist et al. 1988). Neuronal activity was monitored to determine relative depth of physiological landmarks. A dual window discriminator was used to digitize neuronal discharges, and these were stored with stimulus and behavioral event markers using the REX experimental control system (Hays et al. 1982). Neuron responses were averaged across the 1-s period over six to eight stimulus presentations to characterize responses to each stimulus.

Once a neuron was isolated, its approximate receptive field boundaries were determined by a hand-held projector. MSTd neurons were identified by their physiologic characteristics including large receptive fields ($>20° \times 20°$) containing the fixation point, direction-selective responses, and a preference for large moving patterns rather than moving bars or spots (Duffy and Wurtz 1991a,b, 1995; Komatsu and Wurtz 1988). The approximate location within area MST was confirmed with the deeper extension of the penetration across the superior temporal sulcus (STS) to obtain typical responses of medial temporal (MT) neurons. MT was characterized as having greater responsive-

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**FIG. 1.** Stimuli used in these studies. A: pursuit trials consisted of leftward, rightward, upward, or downward pursuit at $15°/s$ for 1 s. Pursuit started $7.5°$ from the center and ended at the same eccentricity on the opposite side. The $76° \times 76°$ optic flow stimuli (fine arrows in smaller boxes) moved with the pursuit target (heavy arrows) on the $91° \times 91°$ projection screen (larger boxes). Fixation trials (not shown) consisted of centered fixation throughout the 1-s visual stimulus period. B: the 9 optic flow patterns consisted of 500 white dots moving at an average speed of $40°/s$ across a dark $90° \times 90°$ projection screen. Straight ahead self-movement was simulated by a centered focus of expansion (FOE) stimulus. The 8 other directions of forward self-movement had FOEs at $30°$ eccentricity and at $45°$ intervals around $360°$. Here, each frame represents the screen containing one of the stimuli with the FOE at the junction of the arrows and the fixation point at the center of the screen. C: triple-plane stimuli had the same FOE location in 3 transparently superimposed sets of dots. Each speed plane contained 166 dots moving at an average speed of $20$, $40$, or $60°/s$, respectively. D: the 3 separate speed stimuli each contained 500 dots moving at an average speed of either $20$, $40$, or $60°/s$. These were used to characterize speed effects on neuronal responses.
ness to bar or spot movement than is seen in MST, with smaller receptive fields that are proportionate to the eccentricity of the receptive field center.

We then recorded responses to all nine FOEs with single- and triple-plane stimuli during centered fixation and pursuit. Blank screen and stationary-dots control trials were randomly interleaved with test stimuli to provide a standard measure of neuronal responsiveness throughout all studies.

**Recording sites**

Neuron recordings in cortical area MST were directed by the stereotaxic positioning of the recording chambers and the depths of microelectrode penetrations. Magnetic resonance imaging (MRI) of the brain, with microelectrodes in place, confirmed positioning in MST. MRIs were obtained in the sagittal plane on a 1.5 Tesla magnet (General Electric) with fast spoiled gradient echo technique (TR = 23.5, TE = 10.3, 30° flip angle). The scans confirmed the location of the electrode tips in the anterior bank of the STS.

On the completion of neuron recording in each monkey, electrolytic lesions (25 μA × 25 s) were made in each hemisphere along penetration tracks in three different guide tubes. After perfusing the animal and fixing the tissue, we cut posterior cortical blocks in 50-μm-thick sections. Nissl and Luxol Fast Blue techniques were used to stain every fourth and fifth section, respectively. The recording sites were identified by extrapolation from the location of the electrolytic lesions. The analysis of histology from the two hemispheres studied indicates that these neurons were in the anterior bank of the superior temporal sulcus that is included in dorsal part of area MST (MSTd) (Komatsu and Wurtz 1988).

**Data analysis**

Trial-by-trial discharge rates for each stimulus condition were averaged across the 1-s stimulus period and entered into ANOVAs using the SAS statistics package (SAS Institute 1988) to quantify the effects of stimulus parameters on neuronal activity. The results were tested for statistical significance at the $P < 0.05$ level.

Neuronal responses were displayed as linear plots to emphasize relative response amplitude and as polar plots to emphasize response directionality. In the polar plots (Fig. 6a), eight thin radial lines represent responses to the optic flow stimuli with FOEs in the direction of the lines. The length of the eight radial lines is proportionate to the neuronal firing rate during the corresponding stimulus period.

The thick radial line in each polar plot indicates the vector sum of the eight individual response vectors. The angle of the net vector is the mean direction of that polar distribution. The length of the net vector, the resultant length, is a measure of the strength of the direction selectivity in that polar distribution. We used circular statistical analyses for data sampled at 45° intervals around 360° (Batschelet 1981), including the Rayleigh Z statistic to test for significant directionality in a circular response profile. A large Z-value suggests a uni-modal distribution with a clearly preferred direction.

**RESULTS**

We studied 134 neurons in the anterior bank of the STS. All neurons were more responsive to the movement of large patterns than to the movement of spots or bars. Most of the receptive fields covered more than a full quadrant of the visual field and included the fixation point as is typical of neurons in the dorsal segment of area MST (Komatsu and Wurtz 1988). All classes of optic flow neurons in MST (Duffy and Wurtz 1991b) were included because all might contribute to heading determination (Duffy and Wurtz 1995) during fixation and pursuit (Page and Duffy 1999). Limitations on recording duration precluded the testing of other flow field stimuli.

**Pursuit reveals planes effects**

We tested whether pursuit disrupts optic flow selectivity and whether such effects are greater with triple-plane stimuli that do not have a visible FOE during pursuit. The single- and triple-plane versions of our nine optic flow fields were presented while the monkey performed pursuit eye movements in four (horizontal and vertical axes, $n = 34$) or two directions (horizontal axis alone, $n = 100$; Fig. 2).

MST neurons respond differently to single- and triple-plane stimuli during pursuit. Figure 3 shows the responses of a neuron with a strong preference for optic flow stimuli having FOEs in the upper visual field. During all directions of pursuit, the triple-plane stimuli with 166 dots in each plane (---) maintained stronger responsiveness and response selectivity than the single-plane stimuli with 500 dots (—). Figure 4 compares planes effects, defined as the differences between single- and triple-plane responses, in fixation (abscissas) and pursuit (ordinates) for the pursuit direction that yielded the largest effects. In the great majority of neurons, pursuit revealed larger planes effects than were observed in fixation. This was true of 63% (85/134) of the neurons when averaging planes effects across the nine FOE stimuli presented.
in fixation versus pursuit (Fig. 4A). This was true of 72% (96/134) of the neurons when comparing the largest planes effect for any FOE in fixation versus pursuit (Fig. 4B). Both of these distributions are significantly asymmetric by the nonparametric sign test for large samples (Fig. 4A, \( z = 3.1, P < 0.002 \); Fig. 4B, \( z = 5.0, P < 0.0001 \)).

These differences between planes effects in fixation and pursuit were tested in each neuron using a three-way ANOVA to determine the effects of viewing condition (fixation vs. pursuit), depth cues (single vs. triple planes), and FOE location (9 FOEs). Half of the neurons (49%, 66/134) showed a significant main effect of depth cues, indicating higher response rates for triple planes or a significant interaction between viewing condition and depth cues, indicating that responses to triple-plane stimuli were larger under conditions of pursuit \( (P < 0.05) \). In many of these neurons (46%, 30/66), the effect of depth planes was restricted to the preferred FOEs as shown by a significant depth planes \( \times \) FOE interaction.

**Multiple planes enhance responses**

Responses to triple-plane stimuli during pursuit were generally larger than the corresponding responses to single-plane stimuli. Figure 5 shows the differences in the magnitude of responses to single- and triple-plane responses during pursuit as a percentage of the single-plane responses during fixation. Averaging across the nine FOE locations, 68% (91/134) of the neurons showed larger triple-plane responses (Fig. 5A, right). Focusing on the FOE that showed the largest planes effect, 71% (95/134) of the neurons showed larger triple-plane responses (Fig. 5B, right). These distributions are highly asymmetric (Fig. 5A, sign test \( z = 4.1, P < 0.0001 \); Fig. 5B, sign test \( z = 5.0, P < 0.0001 \)).
The directionality of single- and triple-plane responses was compared in the 63 neurons that showed significant differences between those responses. The great majority of neurons (70%; 44/63) showing stronger direction selectivity in the triple-plane responses created a highly asymmetric distribution (Fig. 6B, sign test z = 3.2, P < 0.002). In contrast, the direction that was preferred was almost always the same in single- and triple-plane responses. Neurons that showed significant direction selectivity in both single- and triple-plane responses (Rayleigh Z with P < 0.05) rarely (9%, 3/34) showed substantial changes in their preferred direction (Fig. 6C).

Thus during pursuit, triple-plane stimuli evoked larger optic flow responses with stronger direction selectivity than was evoked by single-plane stimuli.

**Speed affects heading responses**

To evaluate the contributions of speed sensitivity to the triple-plane responses, we presented the three component speed planes as separate stimuli. Optic flow stimuli with nine different FOEs were presented at the three speeds of 20, 40, and 60°/s, where the 40°/s stimulus was the single-plane stimulus. Speed effects were mainly seen as larger excitatory responses to the preferred FOE stimuli (Fig. 7A), although larger inhibitory responses to the anti-preferred FOEs were also observed.

We studied 69 neurons with stimuli at 3 speeds during fixation. Figure 7B shows their speed sensitivity measured as the amplitude of their largest response to the nine FOE stimuli at each of the three speeds tested. The largest response to slow (● and ○) and fast (■ and □) stimuli are expressed as a percentage of the largest response to the moderate speed stimuli (100% line). Most neurons (64%, 44/69) preferred the fast speed stimuli, with less than half as many (19%, 13/69) preferring the moderate speed, and still fewer (17%, 12/69) preferring the slow speed.

Directional analysis of these responses showed that MST neurons maintain their preferred directions across stimulus speed changing only the strength of their direction preferences. The vast majority (81%, 56/69) of the neurons showed changes of at least 20% in the resultant lengths of their responses to different speed stimuli. In contrast, only 18% (11/62) of these neurons showed changes of mean direction >20° across stimulus speeds.

The speed preferences of MST neurons were maintained during pursuit, but the strength of their speed preferences varied substantially. Figure 8A shows the responses of an MST neuron to the three sets of speed stimuli presented during leftward pursuit, centered fixation, and rightward pursuit. In all three pursuit conditions this neuron preferred the fast stimuli, but speed effects were strongest during leftward pursuit.

A total of 207 speed studies were conducted (69 neurons and 3 pursuit conditions). The majority of these (59%, 123/207) yielded significant speed effects (2-way ANOVA for speed and FOE, P < 0.05). Significant speed effects were observed in neurons preferring slow, moderate, and fast stimuli in all three pursuit conditions (filled segments of bars in Fig. 8B). However, the majority of neurons consistently preferred the fast stimuli (Fig. 8B).

The pattern of speed sensitivity was maintained across pursuit conditions, although the strength of that sensitivity varied...
substantially (as in Fig. 8A). We made 138 comparisons between pursuit (left or right) and fixation in the 69 neurons studied with speed stimuli under all 3 conditions. In 44\% (61/138) of these comparisons, both the pursuit and fixation responses showed significant speed effects. The vast majority (82\%, 50/61) of these comparisons showed the same preference for slow, moderate, or fast speed stimuli in both conditions.

Thus we find that stimulus speed changes the strength of optic flow responses without changing their direction preferences. In addition, speed sensitivity persisted during pursuit, although the strength of speed preferences varied.

Responses to depth cues
We examined the relationship between speed sensitivity and responses to triple-plane stimuli to determine whether a preference for one speed plane altered responses to multiple, superimposed speed planes. Our approach is illustrated by the responses of a neuron with a strong preference for fast stimuli (Fig. 9A, left). Its responses to the separate presentation of the three speed stimuli were averaged for each FOE (Fig. 9A, right, —) and found to be substantially smaller than its responses to triple-plane stimuli (Fig. 9A, right, —). The peak response with triple-plane stimuli was 22\% larger than the average speed-plane responses, and it was nearly as large as the response to the preferred fast speed-plane stimulus presented alone.

Relationships between the averaged responses to the 3 speed planes and the responses to triple-plane stimuli were tested in 69 neurons recorded during leftward and rightward pursuit. Figure 9B shows differences between the triple-plane and averaged speed responses as a percentage of response amplitude (abscissa) across studies (ordinate). Many studies (41\%, 57/138) showed large differences (>20\%), creating a highly asymmetric distribution (sign test $z = 5.6, P < 0.0001$). Almost all of those with large differences (96\%, 55/57) preferred the triple-plane stimuli.

We tested the significance of differences between responses to triple-plane stimuli and the averaged responses to the speed stimuli. Many neurons (38\%, 26/69) showed significant stimulus effects or stimulus × FOE interaction effects in one or both pursuit directions, most of these (81\%, 21/26) showing larger responses to the triple-plane stimuli. Thus the triple-
plane responses were larger than the averaged responses to the individual speed planes, seemingly maintaining speed preferences even when multiple, speed planes are presented. We considered that the effects of triple-plane stimuli might be limited by a conflict between its motion parallax depth cue and a binocular disparity cue from our flat stimulus screen. We approached this issue by comparing planes effects during monocular viewing and two with lesser effects. Therefore, with binocular viewing, single-plane responses were larger, but during monocular viewing triple-plane responses were larger.

We conducted 67 studies in 21 neurons using single- and triple-plane stimuli with binocular and monocular viewing. Two-thirds (66%, 14/21) showed no changes in planes effects other than a uniform decrease in response amplitude during monocular viewing. The remaining seven neurons included five with greater planes effects during monocular viewing and two with lesser effects. These findings suggest that binocular disparity interacts with speed-defined depth cues in some neurons.

DISCUSSION

Effects of triple-plane stimuli

Pursuit alters the retinal image of optic flow. In single depth-plane stimuli the FOE is displaced from the heading. In multiple depth-plane stimuli there are multiple, overlapping, displaced FOEs (Longuet-Higgins and Prazdny 1980). Paradigmically, heading perception during pursuit is improved by the presence of multiple depth-planes (Royden et al. 1992; Warren and Hannon 1990).

We compared the responses of MST neurons to optic flow stimuli containing 1 speed-defined depth plane with 500 dots or 3 speed-defined depth planes with 166 dots in each plane.
Some differences were observed during fixation, but larger differences emerged during pursuit (Figs. 3 and 4). During pursuit, triple-plane stimuli evoked stronger responses, with stronger direction selectivity, and the same preferred direction (Figs. 5 and 6). Thus as with human observers, multiple speed-defined depth-planes enhance MST neuronal heading selectivity during pursuit.

Enhanced heading perception during pursuit across depth-planes has prompted efforts to identify heading cues other than the FOE. Proposed mechanisms include decomposing optic flow into orthogonal motion components (Koenderink 1986), template matching to motion patterns (Perrone and Stone 1994), and network derivation of heading probabilities (Lappe and Rauschecker 1993). All of these hypotheses are consistent with MST’s neuronal heading selectivity during pursuit (Bradley et al. 1996; Page and Duffy 1999) and our current finding that depth-planes enhance that selectivity. These hypotheses do not predict our finding that speed sensitivity is an important factor.

**Speed sensitivity and pursuit**

The separate presentation of three different speed-planes revealed strong speed sensitivity in most neurons with the largest number (64%, 44/69) preferring the fastest speed (60°/s). The preferred speeds evoked stronger direction selectivity and maintained similar preferred heading directions (Fig. 7). Speed sensitivity persisted during pursuit with about the same proportions of slow, moderate, and fast preferring neurons. However, many neurons showed substantial changes in the strength of their speed sensitivity across pursuit conditions (Fig. 8).

Earlier studies showed that visual speed sensitivity enhances optic flow selectivity in MST (Tanaka et al. 1989). This effect was also seen in studies that detailed MST neuronal tuning for...
a range of speeds (Orban et al. 1995). Both phenomena are important to enhancing responses to optic flow that simulates a particular three-dimensional layout of the visual scene (Duffy and Wurtz 1997). Our current findings show that MST neurons maintain speed sensitivity during pursuit, possibly enhancing stimulus selectivity when multiple depth-planes create a number of flow fields on the rotating retina.

Speed sensitivity during pursuit has several potential advantages. First, greater responsiveness to a particular speed-plane might effectively filter triple-plane stimuli by allowing the preferred speed to dominate the responses. Second, speed sensitivity might cause more neurons to be optimally activated by multiple speed-plane stimuli than by any single speed-plane. Third, the prevalence of fast preferring neurons might cause greater responsiveness to the faster motion in nearer depth-planes where there is less FOE displacement during pursuit.

**Optic flow and depth cues**

Triple-plane responses that are greater than the average response to the component speed-plane stimuli (Fig. 9) might contribute to the perception of motion parallax. Interactions between motion parallax and binocular disparity (Roy et al. 1992) in MST might explain why monocular viewing can enhance differences between single- and triple-plane responses (Fig. 10). We view monocular enhancements as reflecting the removal of conflicts between parallax and disparity cues. This suggests that MST neurons respond to speed-planes as a depth cue and supports our earlier conclusion that MST neurons are sensitive to motion parallax in optic flow (Duffy and Wurtz 1997).

Speed, motion parallax, and disparity sensitivity might all make important contributions to optic flow analysis in MST. The addition of rotation to multiple depth-plane flow fields creates multiple speed-planes on the retina with each speed-plane having a somewhat differently displaced FOE. Each speed-plane might activate a different set of speed-sensitive neurons, each of which would indicate a somewhat different FOE location. Different FOE locations indicated by neurons with different speed preferences might serve as an important signal that there is rotation in the retinal flow field.

MST’s extra-retinal pursuit (Newsome et al. 1988), head movement (Shenoy et al. 1999), and vestibular (Duffy 1998) signals could then be used to apportion flow field rotation to eye, head, and body movements. The remaining rotation would reflect path curvature (Stone and Perrone 1997) that could be assessed using relative depth cues from motion parallax. Finally, the path of self-movement could be derived by scaling to environmental geometry using disparity as an absolute depth cue.

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