Research Article

LEFT-HEMISPHERE DOMINANCE FOR MOTION PROCESSING IN DEAF SIGNERS

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Abstract—Evidence from neurophysiological studies in animals as well as humans has demonstrated robust changes in neural organization and function following early-onset sensory deprivation. Unfortunately, the perceptual consequences of these changes remain largely unexplored. The study of deaf individuals who have been auditorily deprived since birth and who rely on a visual language (i.e., American Sign Language, ASL) for communication affords a unique opportunity to investigate the degree to which perception in the remaining, intact senses (e.g., vision) is modified as a result of altered sensory and language experience. We studied visual motion perception in deaf individuals and compared their performance with that of hearing subjects. Thresholds and reaction times were obtained for a motion discrimination task, in both central and peripheral vision. Although deaf and hearing subjects had comparable absolute scores on this task, a robust and intriguing difference was found regarding relative performance for left-visual-field (LVF) versus right-visual-field (RVF) stimuli: Whereas hearing subjects exhibited a slight LVF advantage, the deaf exhibited a strong RVF advantage. Thus, for deaf subjects, the left hemisphere may be specialized for motion processing. These results suggest that perceptual processes required for the acquisition and comprehension of language (motion processing, in the case of ASL) are recruited (or "captured") by the left, language-dominant hemisphere.

To investigate the perceptual consequences of altered sensory and language input early in development, we studied visual perception in deaf signers who had been auditorily deprived since birth and had acquired a visual language (American Sign Language, ASL) for communication. Although people often say that the deaf "see" better than hearing people (and that the blind "hear" better), only a handful of studies have attempted to systematically investigate the visual capacity of deaf signers. Results from animal studies suggest that visual perception in the deaf may be altered as a result of their auditory deprivation—the auditory-deprivation hypothesis. Alternatively, altered visual perception in the deaf may arise as a result of their acquisition and use of ASL—the ASL hypothesis.

In animal studies, the ability of the developing brain to reorganize itself in response to removal of one of the senses, a phenomenon referred to as cross-modal plasticity, has been clearly demonstrated (see Rauschecker, 1995, and Sur, Pallas, & Roe, 1990). For example, cats blinded from birth (via binocular lid suture) have more cortical neurons devoted to audition than do sighted cats, and furthermore exhibit superior auditory localization abilities (Rauschecker & Kniepert, 1994). Similarly, in cats (Rebillard, Carlier, Rebillard, & Pujol, 1977) and ferrets (Pallas & Moore, 1997) deafened at birth (via strate that brain areas that would normally represent the deprived sense instead come to serve the remaining intact senses. Consistent with the cross-modal neural plasticity observed in ani-

destruction of cochlear receptors), visual responses can be found in

classically defined auditory regions of the brain. These results demon-

mal studies, experiments in humans have suggested that deprivation of input to one modality may lead to compensatory reorganization within intact modalities. For example, several brain-imaging studies of the blind have recorded responses to tactile and auditory stimuli in visual cortex (e.g., Kujala et al., 1995; Rosler, Roder, Heil, & Hennighausen, 1993; Sadato et al., 1996), and these responses may underlie the superior tactile discrimination (e.g., Sadato et al., 1996) and auditory localization abilities (e.g., Lessard, Pare, Lepore, & Lassonde, 1998; Roder et al., 1997) of the blind. Thus, these results in blind humans suggest that visual cortex may come to serve other sensory modalities (i.e., tactile or auditory) when deprived of its normal (i.e., visual) input.

In the deaf, the search for compensatory reorganization has been far more rare, and results have been equivocal. While a study using functional magnetic resonance imagery combined with magnetoencephalography (MEG) found no visual or tactile responses in auditory cortex of a profoundly deaf subject (Hickok et al., 1997), another recent MEG study reported positive results for tactile stimuli (Levänen, Jousmäki, & Hari, 1998). In addition, studies of visual evoked potentials have reported that, compared with hearing people, the deaf show significantly larger visual responses over temporal (and presumably auditory) brain areas (Neville, Schmidt, & Kutas, 1983). Thus, in line with the auditory-deprivation hypothesis, these data suggest that auditory areas in the deaf may be recruited for visual function.

With respect to the perceptual abilities of deaf subjects, most studies have focused on higher level visual-cognitive performance. For example, facial processing (McCullough & Emmorey, 1997); spatial construction and transformation of objects (Bellugi, Poizner, & Klima, 1989); mental transformation, imaging, and rotation (Emmorey, Kosslyn, & Bellugi, 1993); and Gestalt completion (Siple, Hatfield, & Caccamise, 1978) all appear to be superior in deaf signers compared with hearing subjects. In general, these enhanced abilities are thought to be a result of deaf signers' experience with ASL, the comprehension of which relies heavily on such cognitive and visuospatial abilities. Further supporting the ASL hypothesis, many of these studies have demonstrated that hearing offspring of the deaf (i.e., hearing persons who, because they have been born to deaf signing parents, have the same ASL fluency and experience as the deaf) similarly possess such superior abilities.

Relatively fewer deaf studies have addressed more low-level aspects of vision. Temporal discrimination and temporal resolution do not appear to be enhanced in deaf compared with hearing subjects (Mills, 1985; Poizner & Tallal, 1987), yet other aspects of vision, such as the ability to detect and selectively attend to peripheral targets, do seem to be enhanced (Loke & Song, 1991; Neville & Lawson, 1987; Parasnis & Samar, 1985). In sum, surprisingly little is known about visual processing in the deaf, in part owing to the difficult nature of communication between hearing researchers and deaf

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subjects (who speak different languages and are part of different cultures; see Padden & Humphries, 1988), as well as the rarity of these individuals. Moreover, the handful of visual studies conducted with the deaf were not typically designed to selectively activate specific subsystems of vision and therefore could not ascertain at what level of perceptual processing differences between deaf and hearing subjects might exist.

Our study was designed to investigate a single aspect of visual perception in the deaf, specifically, motion processing. We chose motion because deaf signers rely heavily on motion cues for orienting to peripheral objects as well as for comprehending critical linguistic information in the hand movements of ASL. Thus, this aspect of their sensory world may be particularly altered or enhanced. To investigate this possibility, we tested both deaf and hearing subjects on a motion discrimination task in both central and peripheral visual fields.

EXPERIMENT 1

Method

Subjects

Nine deaf signers (mean age = 32 years), recruited from the San Diego deaf community, and 15 hearing subjects (mean age = 22 years), recruited from the student population at the University of California, San Diego, participated in this study. All subjects were right-handed, had normal vision, and were naive to the purpose of the experiment.

Deaf subjects had uncorrected, bilateral, severe to profound hearing loss (>80 dB, based on a questionnaire). All but 2, who became deaf by 2 and 4 years of age, were congenitally deaf. ASL was the primary language of all the deaf subjects and was acquired before age 6 (either from a deaf family member or at a residential school for the deaf). The hearing, nonsigning subjects had normal hearing and no knowledge of ASL.

Stimuli

Motion thresholds were obtained in deaf and hearing subjects, using a stochastic motion display (Newsome & Paré, 1988). This stimulus consists of a field of white dots presented within a circular aperture; some dots (i.e., signal dots) move in a coherent direction (e.g., left or right), while the other dots (i.e., noise dots) move in a random fashion (see Fig. 1a). The proportion of signal dots is varied across trials (2–32%) in order to obtain a coherence threshold (i.e., the percentage of coherent-motion signal yielding 75% correct directional discrimination). The importance of this particular stimulus lies in its ability to selectively activate motion mechanisms while eliminating the use of positional or orientation cues.

Coherence thresholds were obtained for stimuli presented in the central (CVF), left (LVF), and right (RVF) visual fields (duration = 600 ms). Because we predicted that some observed differences between deaf and hearing subjects may be due to the deaf subjects' use of ASL, peripheral stimuli were placed at an eccentricity that approximates where the hands tend to fall in "signing" space at a conversing distance of 5 ft. (Note that the majority of signs fall in the periphery because signers fixate on each other's face). Accordingly, LVF and

RVF stimuli were presented 15° eccentric to fixation in the lower visual field ($x = \pm 7.4^{\circ}$, $y = -13.0^{\circ}$). The stochastic motion display was presented within a 7° circular aperture for CVF stimuli and within a 10° aperture for peripheral stimuli. Signal dots moved at 3.3°/s, in a left or right direction for central stimuli, and in a centrifugal or centripetal direction for peripheral stimuli.

Design and procedure

From a chin rest situated 57 cm away, subjects viewed the video display binocularly. They were instructed to maintain fixation on a small (0.5°) central square throughout the experiment, and report the direction of motion in the stimulus with a key press at the end of each trial (e.g., "left" with a left-hand key or "right" with a right-hand key, in a two-alternative forced choice). Feedback for incorrect responses was provided in the form of a 2.3° white circle briefly flashed above the fixation spot. As a means to discourage eye movements, subjects were told that the experimenter would continuously monitor their eyes via a camera setup.

After 420 trials of practice across all visual fields, subjects were tested with the CVF stimulus. They were then tested with LVF and RVF stimuli, presented in separate and alternating blocks, with the order counterbalanced across subjects. The percentage of coherent-motion signal and motion direction were randomized across trials. In order to obtain thresholds, we fitted psychometric curves to the data, separately for the different field locations. To investigate visual-field asymmetries, we obtained a threshold ratio, LVF_{thr}:RVF_{thr}, for each subject.

Results and Discussion

Psychometric functions and resulting thresholds for 1 deaf subject are shown in Figure 1b, separately for CVF, LVF, and RVF conditions. For this subject, the LVF:RVF threshold ratio was 1.7, indicating an advantage for moving stimuli presented in the RVF.

Coherence thresholds (geometric means) across the 9 deaf signers and 15 hearing nonsigners are presented in Table 1, separately for central and peripheral (averaged over LVF and RVF) conditions. Mean thresholds did not differ significantly between deaf and hearing subjects for either central stimuli, F(1, 22) = 0.22, p = .65, or peripheral stimuli, F(1, 22) = 0.46, p = .50. However, a robust difference between deaf and hearing subjects was found for LVF:RVF threshold ratios. Specifically, deaf subjects exhibited an RVF advantage, whereas hearing subjects exhibited a slight LVF advantage (see Fig. 2a). This difference in threshold ratios between subject groups was significant, F(1, 22) = 5.06, p < .05 (see Table 2 for a list of individual subjects' LVF-RVF asymmetries). Because of the contralateral organization of projections in the visual system, these results imply differential hemispheric advantages for motion processing in deaf versus hearing subjects, with a left-hemisphere specialization in the deaf.

EXPERIMENT 2

In order to confirm these findings, we repeated the motion discrimination task in a second experiment, with several goals in mind. Motion Processing in Deaf Signers

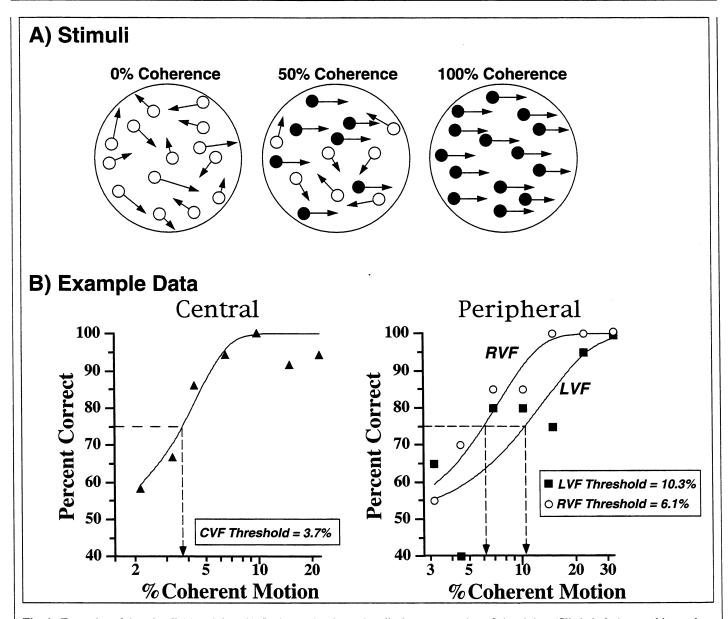


Fig. 1. Examples of the stimuli (a) and data (b). In the stochastic motion display, a proportion of signal dots (filled circles) moved in a coherent direction (e.g., right or left), while the remaining noise dots (open circles) moved in a random fashion. The signal proportion was varied across trials in order to obtain a coherence threshold (i.e., the percentage of coherent-motion signal yielding 75% correct directional discrimination). Dot parameters: luminance = 27 cd/m² against a black (< 1 cd/m²) background; size = 0.12°; density = 2.4 dots/deg²; signal-dot lifetime = 2 frames. Psychometric functions (based on Weibull fits to the data) and resulting thresholds are shown for 1 deaf subject in Experiment 1, separately for the central visual field (CVF), right visual field (RVF), and left visual field (LVF). On average, these functions were derived from 183 trials.

First, we used shorter durations to make the task more difficult, which we thought might reveal differences in absolute thresholds between deaf and hearing subjects. Central stimuli were presented for 400 ms, and peripheral stimuli were presented at two durations for comparison—250 and 600 ms. Second, we presented LVF and RVF stimuli in upper as well as lower visual fields to determine whether the LVF-RVF asymmetry found in Experiment 1 would generalize across visual space. Finally, reaction times (RTs) were recorded to determine whether visual-field asymmetries could be observed for speed of

motion processing. For this purpose, a difference score, $RT_{LVF} - RT_{RVF}$, was determined for each subject.

Method

Subjects

Eight deaf signers (mean age = 33 years), 3 of whom also participated in Experiment 1, and 14 hearing subjects (mean age = 23 years) participated. Criteria for inclusion were the same as for Experiment 1.

Table 1. Mean coherence thresholds in Experiment 1

Subjects	Central stimuli	Peripheral stimulia	
Deaf (n = 9)	2.91	7.33	
Hearing $(n = 15)$	2.31	8.91	

^aData for the lower left and lower right visual fields were averaged.

Stimuli, design, and procedure

Coherence thresholds and RTs¹ were obtained for the stochastic motion display presented in the CVF and in each of the four quadrants of visual space (i.e., lower LVF, lower RVF, upper LVF, and upper RVF).

Unlike in Experiment 1, peripheral stimuli were randomized across trials within a block, thus removing the potential confounding effects of order or practice. The x and y placement of peripheral stimuli (eccentricity = 15.4° , $x = \pm 12.5^{\circ}$, $y = \pm 9.0^{\circ}$) and the display aperture (8°) were thus slightly adjusted from the values in Experiment 1 in order to accommodate stimulus presentation at four different locations on the video display. On each trial, stimulus location was cued by a small (0.3°) white square, which appeared in the to-be-presented stimulus position and disappeared when the trial was initiated. The two duration conditions for peripheral stimuli (i.e., 250 and 600 ms) were presented in alternating blocks, the order of which was counterbalanced across subjects. Other slight differences from Experiment 1 were that signal dots moved at 6.9° /s and all stimuli moved either left or right.

To investigate LVF-RVF asymmetries, we obtained an LVF:RVF threshold ratio (as for Experiment 1) as well as an RT difference score for each subject. Statistical analyses of group mean differences were performed separately for stimuli in the upper versus lower visual field, and for the 250- versus 600-ms duration, as well as for all conditions combined. In all cases, statistical tests that were significant for one duration were significant for the other, and tests that were significant for the upper visual field were also significant for the lower visual field.

Results and Discussion

Coherence thresholds (geometric means) across the 8 deaf signers and 14 hearing nonsigners are presented in Table 3, separately for central and peripheral stimuli. Mean RT data are also presented in Table 3. For central stimuli, as in Experiment 1, mean thresholds did not differ significantly between deaf and hearing subjects, F(1, 20) = 1.61, p = .22; neither did central RTs differ between groups, F(1, 20) = 0.06, p = .81. For peripheral stimuli, however, the deaf exhibited marginally elevated thresholds, F(1, 20) = 4.30, p < .1, and marginally slower RTs, F(1, 20) = 3.95, p < .1. Although this slightly inferior performance could, in principle, be due to the fact that deaf subjects were older, on average, than hearing subjects (F[1, 20] = 8.87, p < .01), post hoc analysis revealed no effect of age on thresholds or RTs (i.e., pair-

Table 2. Individual LVF:RVF threshold ratios in Experiment 1

Hearing subjects		Deaf subjects		
	LVF: RVF		LVF:RVF	
Subject	threshold ratio	Subject	threshold ratio	
S 1	0.78	S1	1.10	
S2	0.24	S2	2.32	
S 3	0.48	S 3	0.60	
S4	0.56	S4	0.68	
S5	1.04	S 5	1.17	
S6	0.82	S 6	0.76	
S7	0.86	S7*	2.38	
S8	0.70	S8* (late)	6.54	
S9	1.03	S9* (late)		
S10	2.03	` ,		
S11	0.61			
S12	1.22			
S13	1.25			
S14	0.92			
S15	0.84			

Note. Asterisks denote subjects who participated in Experiment 2 also. "Late" refers to subjects who were not congenitally deaf, but became deaf by age 4. LVF = left visual field; RVF = right visual field.

wise correlations between age and performance yielded p values > .33 for all conditions), and thus age is unlikely to account for this finding.

Most important, a differential visual-field asymmetry in deaf versus hearing subjects was clearly replicated in Experiment 2 (Fig. 2b, left panel). LVF:RVF threshold ratios were significantly different for hearing versus deaf subjects, F(1, 20) = 16.25, p < .001, and no interaction of group was found with either duration or upper-versus-lower field. As in Experiment 1, an RVF advantage was found for deaf subjects, whereas an LVF advantage was found for hearing subjects. Only for the deaf, however, was the hemifield advantage significant. That is, at both durations, a significant difference between LVF and RVF thresholds held for the deaf (p < .005), thus supporting the hypothesis that there is a strong RVF advantage for motion processing in the deaf.

Table 3. Mean coherence thresholds and reaction times in Experiment 2

	Central stimuli (400 ms)	Peripheral stimulia	
Subjects		250 ms	600 ms
	Coherence threshold	ds	
Deaf (n = 8)	8.11	10.5	9.36
Hearing $(n = 14)$	5.78	7.14	6.38
	Reaction times ^b (ma	s)	
Deaf (n = 8)	751	775	927
Hearing $(n = 14)$	770	675	861

^aData for the lower left, upper left, lower right, and upper right visual fields were averaged.

^{1.} Note that subjects were not informed that their RTs would be recorded, and were therefore not encouraged to sacrifice speed for accuracy or vice versa. In addition, they were not required to wait until the extinction of the stimulus before entering their response.

^bReaction times were measured starting from stimulus onset.

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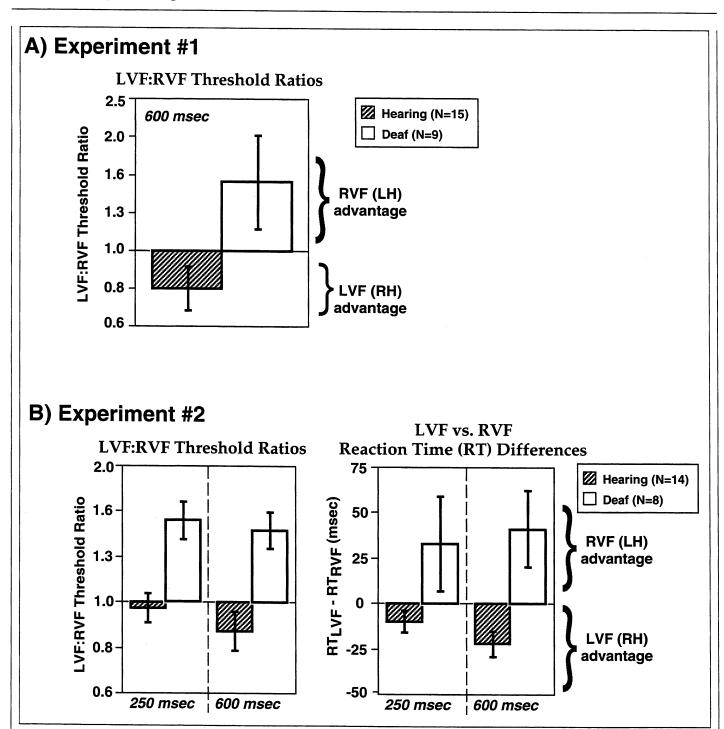


Fig. 2. Left-visual-field (LVF) versus right-visual-field (RVF) asymmetries in Experiment 1 (a) and Experiment 2 (b). Mean LVF:RVF threshold ratios greater than 1.0 indicate better performance for RVF stimuli, and thus a left-hemisphere (LH) advantage. Likewise, values less than 1.0 indicate an LVF/right-hemisphere (RH) advantage. In Experiment 2, reaction time (RT) differences ($RT_{LVF} - RT_{RVF}$) were obtained, in addition to threshold ratios. Because no differences were found between data for the upper and lower visual fields, the data have been combined in the figure. Error bars denote standard errors of the means.

Mean RT differences for LVF versus RVF stimuli show a similar and robust pattern of results, and are plotted in Figure 2b (right panel). For deaf subjects, RTs were shorter for RVF than LVF stimuli, and hearing subjects exhibited an opposite asymmetry. This difference

between groups was significant, F(1, 20) = 9.29, p < .01 (see Table 4 for a list of individual subjects' LVF-RVF asymmetries). Notably, these visual-field asymmetries cannot be explained by speed-accuracy tradeoffs, as faster RTs were paralleled by better performance in all cases.

Table 4. Individual LVF:RVF threshold ratios and reaction time (RT) differences in Experiment 2

Hearing subjects			Deaf subjects		
Subject	LVF:RVF threshold ratio	LVF – RVF RT (ms)	Subject	LVF:RVF threshold ratio	LVF – RVF RT (ms)
S1	0.91	-10.25	S1	1.59	8.25
S2	1.04	-5.75	S2	1.74	11.75
S3	1.19	14.75	S3	1.60	39.00
S4	0.81	-1.50	S4	1.04	15.00
S5	0.90	-18.25	S5	2.53	7.50
S6	0.66	-54.50	S6*	1.79	-10.25
S7	0.60	-56.50	S7* (late)	1.43	175.25
S8	1.52	-35.50	S8* (late)	1.20	47.25
S9	0.99	-34.25	Do (Idio)	1.20	47.25
S10	1.03	-18.50			
S11	1.12	-1.75			
S12	1.30	-5.50			
S13	0.68	-7.00			
S14	1.09	10.25			

Note. Asterisks denote subjects who participated in Experiment 1 also. "Late" refers to subjects who were not congenitally deaf, but became deaf by age 4. LVF = left visual field; RVF = right visual field.

GENERAL DISCUSSION

In sum, the results from our motion studies demonstrate comparable overall performance in deaf and hearing subjects, suggesting that auditory deprivation does not heighten visual abilities in the deaf (at least on this task). Despite the lack of an overall effect, the data nonetheless demonstrate a strong RVF advantage for deaf subjects, and a slight LVF advantage for hearing subjects. Given the contralateral organization of the visual system, these results suggest a left-hemisphere advantage for the deaf and a right-hemisphere advantage for hearing subjects, contributing to the mounting (although somewhat controversial) evidence for hemispheric asymmetries on various visual tasks, such as spatial processing (see Christman, 1997, for a review and for discussion of alternative hypotheses for hemispheric asymmetries unrelated to sensory processing per se).

To our knowledge, this is the first report of hemispheric asymmetries for motion processing in deaf as well as hearing subjects (but see Christman, 1997, for a review of scattered studies in hearing subjects that have yielded negative or equivocal results). Because evidence suggests that the visual language of the deaf is lateralized to the left hemisphere (e.g., Bellugi et al., 1989; Corina, Vaid, & Bellugi, 1992; Neville et al., 1998), as is spoken language for hearing individuals, it is tempting to speculate that the deaf's left-hemisphere advantage for motion processing results from temporal coincidence between visual input and linguistic comprehension. This hypothesis, originally proposed by Neville and Lawson (1987) to account for their finding of a left-hemisphere advantage in the deaf for detection of positional offsets of peripheral targets, supposes that perceptual processes required for the acquisition and comprehension of a language (motion or positional information in the case of ASL) may be "captured" by the left, language-dominant hemisphere. Such a phenomenon could occur in the form of enhanced responses in visual motion areas of the left hemisphere or responsiveness of left-hemisphere language areas to non-language-related motion stimuli. Whatever the exact mechanism may be, the results from these studies appear to be in line with the ASL hypothesis (although future testing of hearing offspring of the deaf will provide an important test of this hypothesis), suggesting that the acquisition of a visual language in the deaf may lead to the reorganization of fairly low-level visual functions, such as motion processing.

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