



Visual cortex entrains to sign language

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Despite immense variability across languages, people can learn to understand any human language, spoken or signed. What neural mechanisms allow people to comprehend language across sensory modalities? When people listen to speech, electrophysiological oscillations in auditory cortex entrain to slow (<8 Hz) fluctuations in the acoustic envelope. Entrainment to the speech envelope may reflect mechanisms specialized for auditory perception. Alternatively, flexible entrainment may be a general-purpose cortical mechanism that optimizes sensitivity to rhythmic information regardless of modality. Here, we test these proposals by examining cortical coherence to visual information in sign language. First, we develop a metric to quantify visual change over time. We find quasiperiodic fluctuations in sign language, characterized by lower frequencies than fluctuations in speech. Next, we test for entrainment of neural oscillations to visual change in sign language, using electroencephalography (EEG) in fluent speakers of American Sign Language (ASL) as they watch videos in ASL. We find significant cortical entrainment to visual oscillations in sign language <5 Hz, peaking at ~1 Hz. Coherence to sign is strongest over occipital and parietal cortex, in contrast to speech, where coherence is strongest over the auditory cortex. Nonsigners also show coherence to sign language, but entrainment at frontal sites is reduced relative to fluent signers. These results demonstrate that flexible cortical entrainment to language does not depend on neural processes that are specific to auditory speech perception. Low-frequency oscillatory entrainment may reflect a general cortical mechanism that maximizes sensitivity to informational peaks in time-varying signals.

sign language | cortical entrainment | oscillations | EEG

Languages differ dramatically from one another, yet people can learn to understand any natural language. What neural mechanisms allow humans to understand the vast diversity of languages and to distinguish linguistic signal from noise? One mechanism that has been implicated in language comprehension is neural entrainment to the volume envelope of speech. The volume envelope of speech fluctuates at low frequencies (< 8 Hz), decreasing at boundaries between syllables, words, and phrases. When people listen to speech, neural oscillations in the delta (1–4 Hz) and theta (4–8 Hz) bands become entrained to these fluctuations in volume (1–4).

Entrainment to the volume envelope may represent an active neural mechanism to boost perceptual sensitivity to rhythmic stimuli (2, 5–7). Although entrainment is partly driven by bottom-up features of the stimulus (8–10), it also depends on top-down signals to auditory cortex from other brain areas. Auditory entrainment is strengthened when people see congruent visual and auditory information (11, 12) and is modulated by attention (13) and by top-down signals from frontal cortex (4, 14).

Cortical entrainment is proposed to perform a key role in speech comprehension, such as segmenting out syllables from a continuous speech stream (1, 2, 15) or optimizing perceptual sensitivity to rhythmic pulses of sound (5–7). However, the mechanisms driving entrainment to speech remain unclear. We consider two hypotheses. First, flexible entrainment to quasiperiodic rhythms may be specific to auditory perception (6); in visual

perception, by contrast, cortical oscillations in the alpha band (8–12 Hz) may phase-lock only to consistent stimulus rhythms, without adjusting to variable stimulus rhythms (16). Second, low-frequency cortical entrainment may be a general-purpose neural mechanism that helps optimize perception to time-varying stimuli regardless of the perceptual modality. Neural oscillations may allow the brain to rhythmically orient attention to quasiperiodic stimuli (5, 17) across sensory systems.

Because previous studies of cortical entrainment to rhythms in language have focused on oral speech, they have been unable to distinguish between these competing hypotheses. Here, we test for low-frequency entrainment to a purely visual language: American Sign Language (ASL). Prior studies have shown that neural and behavioral oscillations in vision are preferentially entrained by stimuli that flicker in the alpha band (18–21). Therefore, if flexible cortical entrainment to oral speech depends on modality-specific properties of auditory processing, then phase-locking to sign language should be concentrated in the alpha band, if it occurs at all (16). Alternatively, if cortical entrainment is a generalized neural strategy to maximize sensitivity to rhythmic stimuli, then oscillatory activity in visual cortex should entrain at the frequency of informational changes in ASL.

To determine whether human cerebral cortex entrains to rhythmic information in sign language, first we developed a metric for quantifying the amplitude of visual change in sign, by analogy to the acoustic envelope of speech. Next, we characterized visual variability across four sign languages, showing that this variability is quasiperiodic at <8 Hz. Finally, we demonstrated that cerebral cortex entrains to visual variability in sign language and showed that entrainment is strongest around the frequencies of phrases and individual signs in ASL.

Significance

Language comprehension is thought to rely on a combination of specialized and general-purpose neural mechanisms. When people listen to speech, low-frequency oscillations in cerebral cortex (<8 Hz) become entrained to quasirhythmic fluctuations in volume. Entrainment of auditory cortex to speech rhythms has been well documented, but its functional significance has remained unclear. By showing similar entrainment of visual cortex to sign language, we establish that this phase-locking is not due to specific properties of auditory cortex or of oral speech perception. Rather, low-frequency entrainment is a generalized cortical strategy for boosting perceptual sensitivity to informational peaks in time-varying signals.

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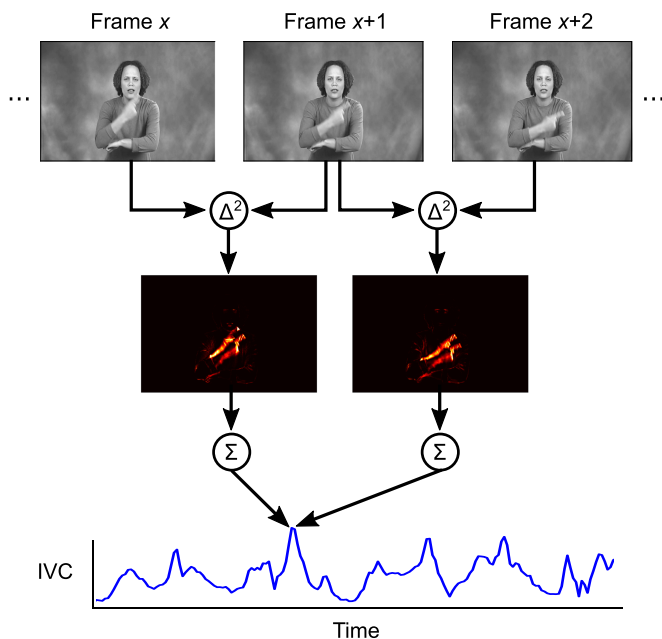


Fig. 1. Calculation of the IVC. The IVC summarizes total visual change at each point in time. First, the difference between adjacent grayscale video frames (Top) is calculated for each pixel. To aggregate over both increases and decreases in brightness, these pixel-wise differences are then squared (Middle). Finally, the brightness values in all pixels of the squared-difference images are summed to obtain a single value summarizing the magnitude of change between two video frames. Computation of this value for each adjacent pair of frames yields a time-series (Bottom).

Results

Developing a Metric for Quantifying Visual Change. To examine neural entrainment to visual rhythms in sign language, we must first quantify the “amplitude envelope” of a visual signal. The acoustic envelope is a highly reduced representation of sound, tracing extreme amplitude values in the time-varying signal. Oscillations in the envelope of speech depend on movements of various components of the vocal tract, including the rhythmic opening and closing of the mandible (22). Sign language, in contrast, does not involve consistent oscillatory movements by any single effector (23). However, quasiperiodic oscillations in sign language may arise from the coordinated movements of multiple effectors.

Here we present the Instantaneous Visual Change (IVC) as a metric that is conceptually similar to the acoustic envelope, summarizing the amplitude of change at each time point. The IVC is a time series of aggregated visual changes between frames (Fig. 1 and *Method and Materials*). This algorithm provides an automatic, objective alternative to human-coded methods of studying temporal structure in sign (24).

The amplitude of the IVC indexes the amount of visual change between two video frames. The largest peaks in the IVC therefore occur during large, quick movements. In the videos we analyzed, these changes corresponded primarily to movements of the signers’ hands and arms, but may also reflect movements of the face, head, and torso. For example, a quick arm movement results in a larger number of pixels changing in each adjacent frame—and a higher peak in the IVC—than a slow arm movement. The IVC thus offers a heuristic index of linguistic information in the visual signal. An example movie illustrating the IVC is included as [Movie S1](#).

Characterizing Temporal Structure in Sign Language. The IVC allows us to characterize one dimension of the temporal structure

of sign language and to directly compare the spectral signatures of amplitude variability across sign and oral speech. Visual examination of the raw IVC of sign language reveals quasiperiodic oscillations with irregularly timed peaks (Fig. 2A). To characterize variability within and across sign languages, we computed the power spectra of the IVC from samples of four different sign languages: American Sign Language (ASL), German Sign Language (Deutsche Gebärdensprache; DGS), British Sign Language (BSL), and Australian Sign Language (Auslan). These languages developed independently of the oral languages spoken in these countries and come from three genetically unrelated language families (BSL and Auslan from the British, Australian, and New Zealand Sign Language family; ASL from the French Sign Language family; and DGS from the German Sign Language family). In all four languages, power in the IVC decreases roughly monotonically with increasing frequency, without any pronounced peaks in the spectrum (Fig. 2C). We tested for rhythmic components in the IVC by comparing these spectra against the $1/f$ spectrum characteristic of many signals in the natural world. Power that is higher than the $1/f$ function indicates periodicity at that frequency (22). The IVC of sign language showed elevated power at $\sim 2\text{--}8$ Hz ($P_s < .01$). Individual signs in sign languages tend to occur at $\sim 2\text{--}2.5$ Hz (25, 26), on the lower end of the rhythmic components in the IVC. These analyses suggest that sign language involves weak, quasiperiodic rhythms with variable frequencies in the delta and theta range.

To explicitly compare temporal structure between sign and speech, we contrasted the IVC of sign with the broadband envelope of speech (22). We computed the broadband envelope

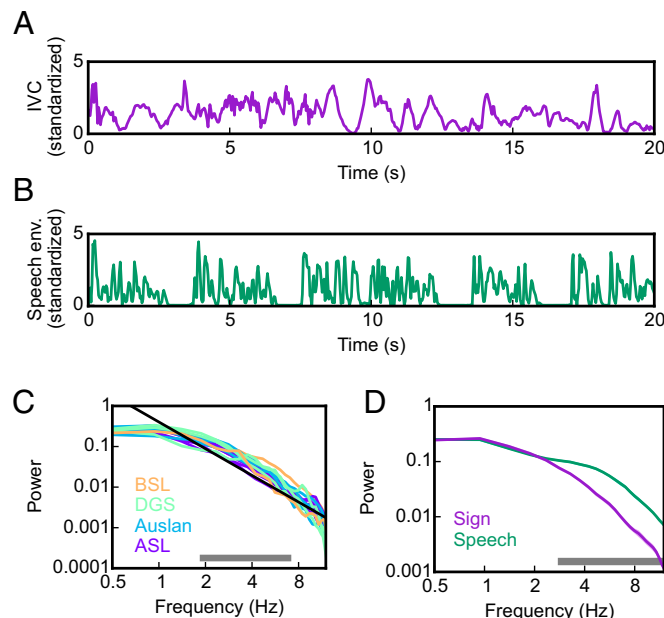


Fig. 2. Temporal structure in signed and spoken language. (A) Example trace of the IVC of ASL. (B) Example trace of the broadband envelope (env.) of English. (C) Spectrum of sign language plotted on log-log axes. Line color denotes language. Each curve shows the spectrum of a separate video sample ($N = 14$; total duration 1:10:22). The black line shows the best-fit $1/f$ trend across all samples. The gray bar at the base of the plot shows where the IVC spectra are significantly greater than the $1/f$ fit ($P < .01$ by one-sample t tests). (D) Comparison of the mean spectra across signed and spoken languages. Shaded area depicts the SE of the mean. The gray bar indicates significant differences between the two curves ($P < .01$ by independent-samples t tests). Sign language samples are the same as in C. Audio recordings were sampled from speech in nine languages ($N = 12$; total duration 1:07:28). Amplitude in all analyses has been standardized by each recording’s SD.

of samples from nine spoken languages representing five language families: English, French, Portuguese, Dutch, German, Hungarian, Japanese, Arabic, and Mandarin. After resampling the broadband envelopes and IVC signals to a common frequency (30 Hz) and standardizing the amplitude of each recording by dividing out its standard deviation, we compared the average spectra of the IVC of sign and the broadband envelope of speech (Fig. 2D). Spoken languages showed stronger modulations than sign languages at >2 Hz. This increased power may reflect modulation due to syllables in speech, which occur at ~2–10 Hz (22, 27). Indeed, peaks from individual syllables are visible in the broadband envelope, and these peaks occur at ~4 Hz (Fig. 2B). These results indicate that visual motion in sign language is modulated at lower frequencies than auditory volume in spoken language. This difference is consistent with the slower movements in the articulators for sign (the hands) than in the articulators for speech (the vocal tract) (25, 26).

Cortical Coherence to Visual Rhythms in Sign Language. We used electroencephalography (EEG) to examine cortical entrainment to quasirhythmic fluctuations in visual information in sign language. Fluent speakers of ASL watched videos of ASL stories against a static background. We tested for coherence of low-frequency electrophysiological oscillations to quasiperiodic oscillations in the IVC.

Coherence was calculated separately at each EEG channel in partially overlapping, logarithmically spaced bins centered over 0.5–16 Hz (*Materials and Methods*). Because coherence provides no intrinsic measure of chance performance, we created a null distribution of coherence using a randomization procedure. To obtain each value in the null distribution, we time-shifted the IVC to a randomly selected starting point, moving the portion of the IVC that remained after the final time point of the EEG signal to the beginning of the recording. This procedure preserves the spectral and temporal characteristics of the EEG and IVC recordings, but eliminates any relationship between these signals. Coherence was then computed between the EEG recordings and the randomly shifted IVC.

A cluster-based permutation test indicated that coherence between cortical oscillations and the IVC of sign was stronger than would be expected by chance ($P = .0001$). Averaging the coherence spectrum across every EEG channel, coherence was above chance from 0.4 to 5 Hz, peaking at 1 Hz (Fig. 3A).

Coherence emerged over a similar range of frequencies when we selected only occipital channels (0.8–5 Hz; $P = .0001$), primarily reflecting entrainment in visual cortex (Fig. 3B). In frontal channels, above-chance coherence was present from 0.4 to 1.25 Hz ($P = .0001$; Fig. 3C), revealing top-down control from frontal cortex. Examining the entire scalp distribution, cortical coherence to the IVC of sign language was strongest over central and occipital channels (Fig. 3D).

To test whether cortical entrainment depends on linguistic knowledge, we examined coherence to sign language in people who did not know any ASL. Like signers, nonsigners showed significant coherence to videos of ASL storytelling ($P < .0005$), with the strongest coherence over central and occipital channels from 0.8 to 3.5 Hz (Fig. S1). We then separately analyzed effects of linguistic knowledge on entrainment in occipital and frontal cortex. Although coherence at occipital channels did not significantly differ between groups (Fig. 4B), coherence at frontal channels was stronger in signers than in nonsigners, indicating differences in top-down control based on familiarity with ASL ($P < .05$; Fig. 4A and Fig. S1).

Discussion

Cortical Coherence to Sign Language. In this study, we find that electrophysiological oscillations in human cerebral cortex become entrained to quasiperiodic fluctuations of visual movement in sign language. In fluent signers, cortical entrainment to sign language was found between 0.4 and 5 Hz, peaking at ~1 Hz, and emerged most robustly over occipital and central EEG channels. These results show that the human brain entrains to low-frequency variability in language whether it is perceived with the ears or eyes. Visual cortex flexibly phase-locks to visible changes in sign language, analogously to the way auditory cortex phase-locks to amplitude changes in oral speech. Our findings argue that flexible entrainment depends on mechanisms that are not specific to any given effector or sensory modality.

Prior results suggest that auditory and visual perception are differentially modulated by rhythms at different frequencies (16). Auditory sensitivity varies as a function of the power and phase of spontaneous 2- to 6-Hz rhythms (28), and these oscillations are entrained by sounds modulated at 3 Hz (29, 30). Visual sensitivity, by contrast, depends on the power and phase of spontaneous alpha rhythms (31–33), and electrophysiological oscillations in visual cortex are robustly entrained by periodic

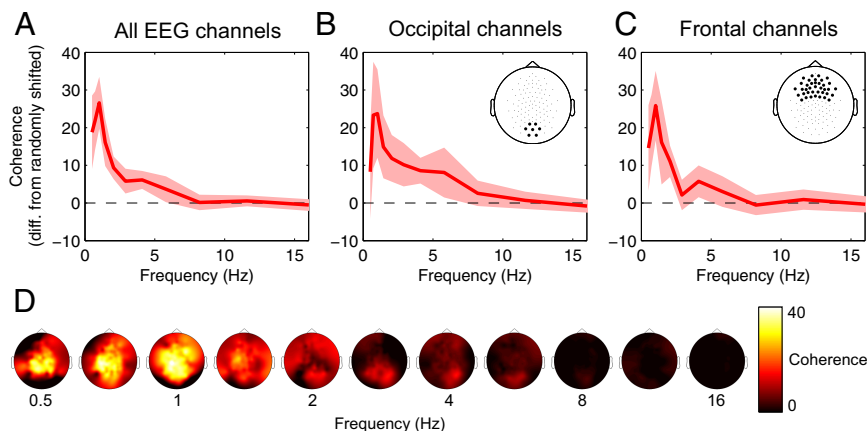


Fig. 3. Coherence between cortex and the IVC of sign language in fluent signers ($N = 13$). (A) Coherence spectrum averaged across all EEG channels. For each participant, we computed the difference in empirical coherence and a distribution of cortical coherence to randomly shifted IVC. The solid line shows the mean difference in empirical and randomized coherence across participants, and the shaded area shows the 95% CI around the mean. The dashed line shows chance levels. (B) Coherence spectrum averaged over occipital channels. *Inset* shows the location of selected channels. (C) Coherence spectrum averaged over frontal channels. *Inset* shows the location of selected channels. (D) Scalp topography of coherence in each frequency bin, averaged across participants. Diff., difference.

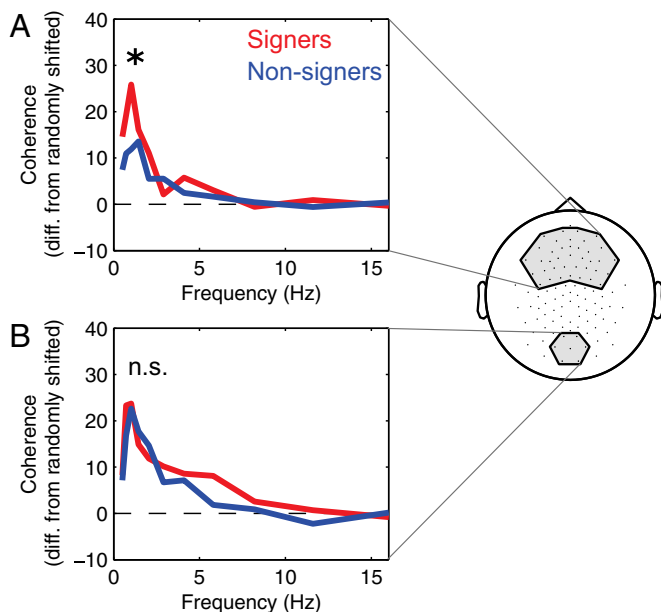


Fig. 4. Comparison of coherence in fluent signers ($N = 13$) and nonsigners ($N = 15$). (A) Coherence at frontal channels (channel selection illustrated at right) was stronger in signers than in nonsigners. (B) Coherence at occipital channels did not differ between groups. Data from signers is the same as in Fig. 3. $*P < .05$; n.s., not statistically significant. Diff., difference.

stimulation at ~ 10 Hz (19, 21). When humans watch a light flicker at frequencies from 1 to 100 Hz, visual cortex shows the strongest entrainment at ~ 10 Hz (18).

Although these rhythmic preferences are not absolute [visual cortex also shows rhythmic oscillations in the delta/theta range (11, 17, 34–37)], differences between the sensory modalities are apparent when different frequency bands are directly compared. Auditory detection sensitivity depends on the phase of underlying delta–theta, but not alpha, oscillations (28). In response to aperiodic stimulation, visual cortex oscillates in the alpha band (20), whereas auditory cortex does not show consistent oscillatory activity (38).

If sensory-specific oscillatory preferences determine the spectrum of entrainment, then peak coherence to sign language should be observed at the frequencies preferred by visual cortex: ~ 10 Hz. Contrary to this prediction, we find that cortical coherence to sign language only emerges at < 5 Hz. Cerebral cortex entrains to sign language around the frequencies of words and phrases in ASL.

Coherence Across Signers and Nonsigners. We find that cerebral cortex phase-locks to visual changes in ASL both in fluent signers and in people with no knowledge of sign language. In principle, coherence to ASL in nonsigners could emerge for two reasons. Coherence could be driven either bottom-up, by sensory stimulation, or top-down, by nonlinguistic temporal predictions. Human bodies move in predictable ways, and nonsigners could entrain to sign language based on these regularities in human movement.

In frontal areas, fluent signers showed stronger coherence than nonsigners. This difference in frontal coherence may reflect top-down sensory predictions based on knowledge of ASL. Alternatively, differences in coherence could reflect differences in attention to the videos. Cortical entrainment to oral speech decreases when people direct attention away from the speech stimulus (13, 39). Reduced coherence in nonsigners, therefore, would also be predicted if nonsigners do not attend to videos of ASL as strongly as fluent signers do. However, our findings at occipital channels argue against this possibility. If differences between

groups were driven by attention, then occipital coherence should be stronger in signers than in nonsigners. However, we find no evidence that occipital coherence depends on linguistic knowledge. Together, these results suggest that, although linguistic knowledge is not necessary for entrainment, signers may leverage knowledge about ASL to sharpen temporal predictions during language comprehension. These sharpened predictions result in stronger entrainment in the frontal regions that exert top-down control over visual perception.

Specialization for Speech? Syllables in oral speech occur at frequencies that largely overlap with cortical entrainment to the volume envelope. This overlap could be interpreted as evidence for a specialized oscillatory mechanism for speech comprehension. This type of speech-specific mechanism could evolve in at least two ways. First, as Giraud and Poeppel state: “The articulatory motor system [may have] structured its output to match those rhythms the auditory system can best apprehend” (6). Second, auditory mechanisms may have developed to comprehend speech based on the timing of preexisting oral behaviors. Non-human primates create vocalizations and facial displays that fluctuate at frequencies similar to human speech syllables (40), and their attention is preferentially captured by faces that move at these frequencies (41); perhaps auditory processing evolved to fit the timing profile of these behaviors.

The data we report here, however, suggest that entrainment may not have any close evolutionary link to oral speech. Instead, a more general process may underlie cortical phase-locking to variability in language. Previous results are consistent with this interpretation as well. When participants watch videos of speech, entrainment emerges not only in auditory cortex, but also in visual cortex (11, 35, 36). Furthermore, cortical rhythms entrain to rhythms in music (42) and to other rhythmic stimuli in audition (29, 30) and vision (19, 43). These examples of low-frequency cortical entrainment to a broad range of stimuli across sensory modalities suggest that the cortical mechanisms supporting entrainment to the volume envelope of speech may be a specialized case of a general predictive process.

Neural Mechanisms of Language Comprehension Across Sensory Modalities. Previous studies have shown that the functional neuroanatomy of speech largely overlaps with that of sign (44). At the coarsest level of anatomical specificity, the left hemisphere is specialized for spoken language. The left hemisphere is also asymmetrically active during sign language perception (45) and production, regardless of which hand people use to sign (46, 47). Left hemisphere damage, furthermore, results in linguistic deficits in signing patients (48).

Specific regions within the left hemisphere show similar involvement in processing both speech and sign. Across signed and spoken language, bloodflow increases to the left inferior frontal gyrus (LIFG) and left inferior parietal lobe (IPL) during phonemic discrimination (49, 50) and morphosyntactic processing (51). Similarly, word production in both signed and spoken languages activates LIFG, left IPL, and left temporal areas (52).

Differences in the cortical areas involved in sign and speech can often be attributed to differences in the form of these languages. For example, comprehension of sign language activates primary visual, but not primary auditory, cortex (45). Consistent with the fact that sign language relies on spatial contrasts, inferior and superior parietal cortex is more strongly active during signed than during spoken language production (52) and perception (49).

Our findings go beyond functional neuroanatomy to examine neurophysiological processes that can arise in multiple cortical areas. We show that oscillatory entrainment to low-frequency variability in the stimulus occurs, regardless of whether language is being processed using auditory cortex or visual cortex.

Our results differ from previous studies on entrainment to speech primarily in the scalp topography of coherence. Entrainment to auditory speech is strongest over auditory cortex (2, 8, 11, 35) and central frontal sites (14). By contrast, our results show that entrainment to sign language is strongest at occipital and parietal channels, consistent with greater parietal activation during sign compared with speech (53). This difference likely reflects increased visual and spatial demands of perceiving sign language.

The IVC Quantifies Temporal Structure in Visual Perception. The IVC provides a method for examining gross temporal structure in natural visual stimuli. Analogously to the way the broadband envelope summarizes early stages of auditory processing, the IVC provides a first approximation of the magnitude of information available to the earliest stages of visual processing. At the first stage of auditory transduction, hair cells in the cochlea extract the narrowband envelope of sounds. Summing these narrowband envelopes together yields the overall auditory responses over time: the broadband envelope. In the retina, center-surround retinal ganglion cells respond to changes in the brightness of specific wavelengths of light. Summing the responses from these cells yields the overall visual responses over time, approximated by the IVC.

The IVC provides a coarse index of visual information in sign language, just as the broadband envelope provides a coarse index of information in speech. For example, the volume envelope does not reflect small spectral differences that are crucial for discriminating vowels. The IVC, analogously, does not preserve information about which effectors are moving or their trajectories. Nevertheless, sign language comprehenders may use the IVC of sign heuristically, as listeners use the acoustic envelope of speech, to anticipate when important information is likely to appear.

In the present study, we use the IVC to characterize temporal structure in sign language and to examine responses of the human brain to that temporal structure. The IVC could also be applied to study temporal structure in other domains, such as gesture, biological motion, and movement in natural scenes.

The Functional Role of Entrainment to Language. Oscillatory entrainment to language may be a specific case of a general cortical mechanism. In primates, spiking probability varies with the phase of low-frequency oscillations: Neurons are most likely to fire at specific points in the phase of ongoing oscillations (54, 55). Perhaps the cortex strategically resets the phase of ongoing neural oscillations to ensure that perceptual neurons are in an excitable state when new information is likely to appear (5–7, 14). Oscillatory entrainment may constitute a cortical strategy to boost perceptual sensitivity at informational peaks in language. Our findings suggest that the brain can flexibly entrain to linguistic information regardless of the modality in which language is produced or perceived.

Materials and Methods

Participants watched ~20 min of naturalistic storytelling in ASL while EEG was recorded. Participants were instructed to watch the videos and remain

still and relaxed. All procedures were approved by the Institutional Review Board of the University of Chicago. Detailed methods and analyses are available in *SI Materials and Methods*.

Participants. Participants had corrected-to-normal vision and reported no history of epilepsy, brain surgery, or traumatic brain injuries. Informed consent was obtained before beginning the experiment, and participants were paid \$20/h for their participation. We recorded EEG from 16 fluent signers of ASL. Data from two participants were excluded before analysis due to excessive EEG artifacts, and data from one participant were lost due to experimenter error. All participants retained in the analyses began learning ASL by 5 y of age ($N = 13$; 3 female, 10 male; age 24–44; mean age of acquisition 1.1 y). Participants who used hearing aids or cochlear implants removed the devices before beginning the experiment. A fluent speaker of ASL (J.L.) answered participants' questions about the study. We recorded EEG from an additional 16 participants who had no prior exposure to ASL. These participants were recruited from the University of Chicago community through online postings. One participant who was currently learning ASL was excluded before analyses, leaving $N = 15$ nonsigning participants (10 female, 5 male; ages 18–31).

IVC. The IVC represents a time-series of aggregated visual change between frames (Fig. 1) and is computed as the sum of squared differences in each pixel across sequential frames of video:

$$\text{IVC}(t) = \sum_i [x_i(t) - x_i(t-1)]^2,$$

where x is the grayscale value of pixel i at time t . Python code for the IVC is available at <https://github.com/gbrookshire/ivc>.

EEG Analysis. See *SI Materials and Methods* for details about EEG acquisition and preprocessing. To compute coherence, IVC and EEG data were filtered into overlapping log-spaced frequency bins by using phase-preserving forward-reverse Butterworth bandpass filters. Bins were centered on values from 0.5 to 16 Hz and included frequencies in the range $(0.8f, 1.25f)$, where f is the center frequency $f = 2^n$ for $n \in \{-1, -0.5, 0, \dots, 4\}$. Instantaneous phase and power were determined with the Hilbert transform. Power was computed as the absolute value of the analytic signal, and phase as the angle of the analytic signal. These power and phase estimates were then used to calculate coherence:

$$\text{Coh} = \frac{|\sum_t (e^{i\theta_t} \sqrt{P_{C,t}} \cdot P_{V,t})|}{\sqrt{\sum_t (P_{C,t} \cdot P_{V,t})}},$$

where t is the time point, θ is the phase difference between the IVC and EEG, P_V is power in the IVC, and P_C is power in the EEG recording (9). Statistical significance of coherence was determined by a two-stage randomization procedure. First, the IVC was randomly shifted to obtain a null distribution of coherence between the two signals. Second, statistical significance was determined by using cluster-based permutation tests (56) (*SI Materials and Methods*).

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