A Rhesus Monkey With a Naturally Occurring Impairment of Disparity Vergence. I. Behavioral Comparisons to Vergence in a Normal Animal

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PURPOSE. Human children with disorders affecting vergence eye movements have difficulty during close work, such as reading. Patients with convergence insufficiency show a receded near point and an exophoria that is greater at near than at far. Neurologic abnormalities may underlie these symptoms, but it is difficult to test this idea directly because there is no animal model for this disorder. In the present case report, we describe behavioral testing in a rhesus monkey with a naturally occurring impairment of vergence eye movements (monkey CI).

METHODS. Three monkeys were trained to perform a variety of oculomotor tasks that required saccades, vergence, and/or smooth tracking of a visual target moving in depth.

RESULTS. Two of the monkeys (N1 and N2) were able to perform these tasks correctly. The third, monkey CI, was able to correctly perform these tasks when the required vergence angle was ≤5° but had difficulty when the task required larger convergence. This animal showed a consistent exodeviation that worsened as the target drew closer. When a variable prism was used to test disparity vergence in monkey CI, the animal showed an unstable convergence response (maximum 6°) that increased with prism correction, up to 12 prism diopters. By comparison, monkey N1 was able to achieve stable, appropriate convergence up to 26 prism diopters. Monkey CI's performance on vergence tasks improved when a large-field random checkerboard pattern was used to provide additional depth cues.

CONCLUSIONS. Monkey CI appears to have a naturally occurring disorder of vergence eye movements.

Keywords: convergence insufficiency, monkey, convergence, vergence

Convergence insufficiency is a common disorder, characterized by a receded near point of convergence (NPC), with an intermittent exophoria that typically worsens after prolonged close work.[1] In young children, these symptoms often interfere with schoolwork, particularly reading.[2–4] In normal children, the NPC is 5 to 10 cm from the bridge of the nose. In patients with convergence insufficiency the break point (i.e., the distance at which appropriate convergence cannot be achieved and an exophoria becomes manifest) can be anywhere from 10 to 30 cm.[1]

To date, progress toward understanding this disorder has been impeded by the lack of an animal model, which makes it difficult to test hypotheses related to possible neural abnormalities. In this case study, we report behavioral data from a rhesus monkey (*Macaca mulatta*) with a naturally occurring impairment of disparity vergence. This animal easily learned to perform a saccade task on a tangent screen at a distance of 57 cm but showed markedly poor performance on a range of oculomotor tasks when more than ~6° of convergence was required. Testing with a Risley prism revealed a clear impairment of disparity vergence.

The primary goal of the present study was to assess the vergence-impaired monkey's performance on a variety of oculomotor tasks. Of particular interest was the question of what factors influence the animal's performance on vergence tasks. Specifically, we compared the animal's response to a pure disparity stimulus, her ability to maintain an appropriate convergence when presented with a large field stimulus at near, performance on a saccade-vergence task, and the gain of vergence smooth pursuit of a target moving in depth.

METHODS

Subjects and Surgical Procedures

Data were collected from three rhesus macaque monkeys (*Macaca mulatta*), including two normal animals (N1 and N2) and one male that showed impaired performance on a range of vergence eye movement tasks, despite normal performance on a saccade task (monkey CI1).

To prepare the monkey for experiments, two sterile surgeries were performed in a dedicated surgical suite. All procedures complied with the National Institutes of Health Guide for the Care and Use of Laboratory Animals and the ARVO Statement for the Use of Animals in Ophthalmic and Vision Research. The Institutional Animal Care and Use Committee at University of Washington approved the protocols.
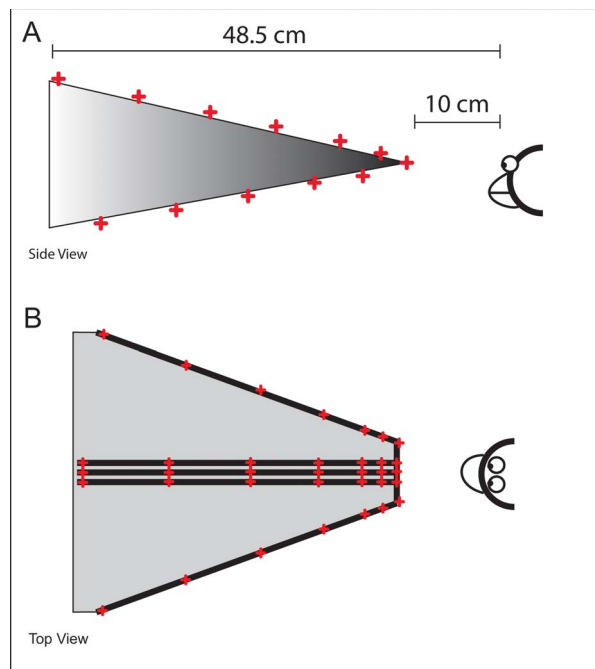
FIGURE 1. Schematic representation of the target array used for the saccade-vergence task. Sixty red, plus-shaped LEDs were arranged along the tops and bottoms of five circuit boards. Targets appeared in 5 different directions and 12 different distances (minimum target distance, 10 cm). Panel (**A**) shows a side view, and (**B**) shows a top-down view. The monkey cartoons have the same orientation. Thus, we are viewing the monkey from the side in panel (**A**), and from a position above the top of the head in panel (**B**).

Surgical procedures were identical to those described in previously published studies.[5,6] A titanium post (Crist Instruments Co., Inc., Hagerstown, MD, USA) was affixed to the skull to permit restraint of the head during experiments. A recording chamber was installed over a 16-mm craniotomy. The chamber was positioned so that the supraoculomotor area could be reached with electrode tracks near the center of the chamber (see companion paper). To permit recording of eye position, eye coils were implanted in both eyes, underneath the conjunctiva.[7,8]

Behavioral Tasks and Visual Display

All experiments were conducted with the head restrained, with the animal in a specially designed primate chair situated at the center of a 1.5-m magnetic coil frame.

Target Step Saccade Task. Monkey CI1 was first trained to make saccades to track a 0.25° laser spot as it stepped to various locations on a tangent screen, at a distance of 57 cm. Possible target locations were chosen by randomly combining horizontal and vertical coordinates (−20° to 20°, in 2° increments). The tasks described below were not used until the animal had been proficient on the target step task for more than 6 months.

Saccade-Vergence Task. For this task, the animal viewed one target at a time in an array of 60 red, plus-shaped LEDs, situated at 12 different distances as follows: 10.2 cm, 11.0 cm, 11.9 cm, 13.1 cm, 14.4 cm, 16.0 cm, 18.1 cm, 20.7 cm, 24.2 cm, 29.0 cm, 36.3 cm, and 48.5 cm (Fig. 1). All targets subtended 1° of visual angle. The targets were arranged along the top and bottom of five triangle-shaped circuit boards, with the closest target on each board positioned at eye level. One circuit board was aligned with the animal's midsagittal plane.
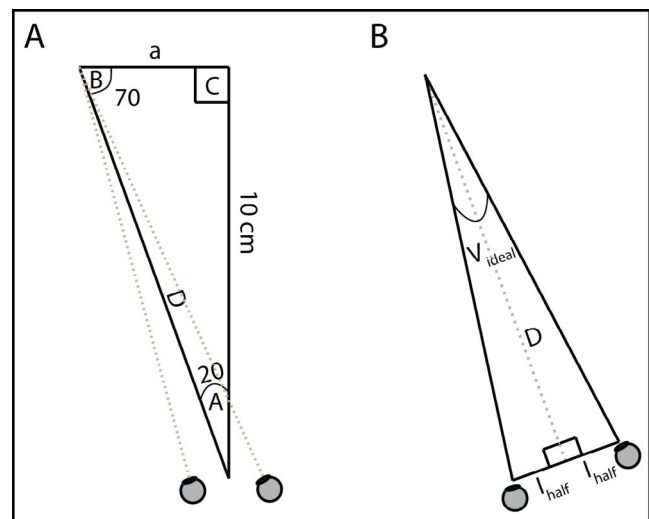

FIGURE 2. Schematic representation of the geometric relationships used to compute the ideal vergence angle for different fixation locations on a large-field checkerboard pattern, presented at a distance of 10 cm. A, the radial eccentricity (in degrees) for a given fixation location; a, physical distance (in cm) of the current fixation location from the straight-ahead position on the tangent screen; D, the distance (in cm) between the intermediate point between the monkey's two eyes and the currently fixated screen location; I_{half}, half of the monkey's interpupillary distance; V_{ideal}, the ideal vergence angle for the current fixation location. See Methods section for the relevant equations.

The absolute distance between the boards was adjustable, so that one could be aligned with the right eye and one with the left. The circuit boards on the far left and far right were positioned at an angle, to ensure that all targets could be seen by both eyes.

During an experiment, one LED was illuminated at a time. The animal was given a small amount of applesauce every 300 to 500 ms for maintaining fixation with both eyes within a 2° circular window around the desired position. The desired position of each eye was computed using basic geometry, based on the two-dimensional eye position signal from the eye coils, the monkey's interpupillary distance, and the known positions of the LEDs in three-dimensional space.

Near Fixation Task. A 14 × 14-cm black and white checkerboard pattern was positioned directly in front of the animal, at a distance of 10 cm with the recording booth illuminated. For this task there was no specific target; the animal was simply rewarded for maintaining a vergence angle greater than 10°, regardless of the direction of gaze. The purpose of this task was to assess the animal's ability to maintain convergence on a full-field target at near, under conditions that were at least somewhat analogous to a human child reading a book.

Smooth Vergence Tracking Task. A single red, plus-shaped LED was positioned on a movable platform, driven by a high precision linear motion actuator (Zaber Technologies, Inc., Vancouver, BC, Canada). The direction of motion was aligned with the animal's midsagittal plane, which elicited smooth, symmetric vergence tracking. The target moved at a constant velocity, following a triangle wave pattern. The frequency ranged from 0.05 to 0.2 Hz. Some experiments were conducted with the recording booth dimly illuminated, with the target surrounded on three sides (top, left, and right) by a 15 × 15-cm black and white checkerboard pattern. This was done to provide monkey CI1 with a more robust set of disparity and accommodation cues. Without this background,
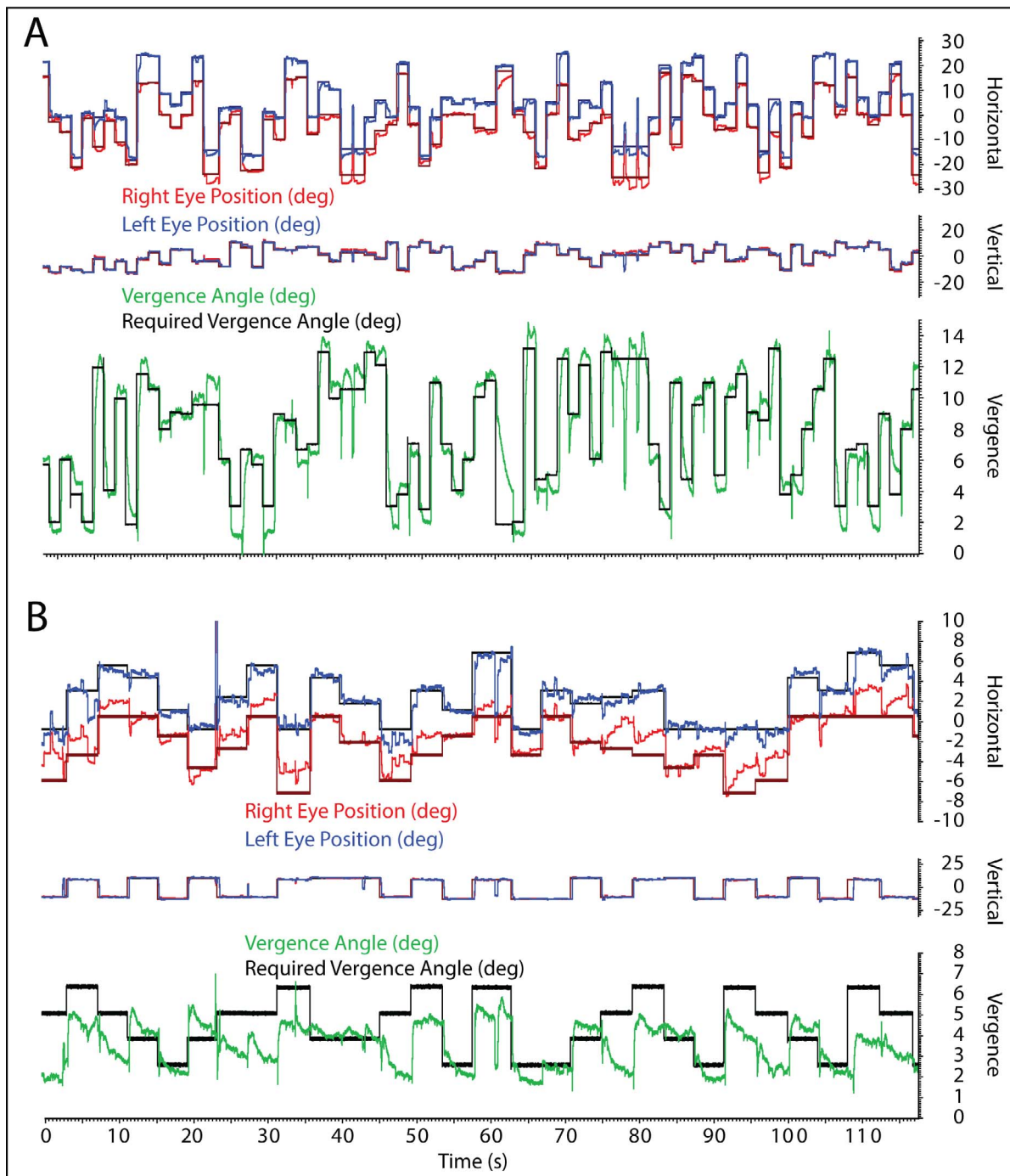
FIGURE 3. Two minutes of raw data during performance of the saccade vergence task for a normal monkey (**A**) and monkey CI (**B**). Note that monkey CI consistently attempted to fixate the target but was unable to bring both eyes to the target when the required vergence angle exceeded ~5°. Note, also, the consistent divergence drift following converging saccades.

monkey CI1 was unable to bring both eyes to the target when more than ~6° of convergence was required.

Data Analysis

Spike 2 software (Cambridge Electronic Design, Cambridge, UK) was used for data acquisition, for visualization of raw data during the experiment, and for preliminary offline analyses. Detailed quantitative analyses were conducted using custom functions written in Matlab (Mathworks, Natick, MA, USA).

The instantaneous velocity of each eye was estimated using 7-point parabolic differentiation of the position signals from the eye coils. Vergence velocity was then computed as:

$$\dot{Verg} = \dot{H}_{Left} - \dot{H}_{Right}$$

where $\dot{Verg}$, $\dot{H}_{Left}$, and $\dot{H}_{Right}$ represent vergence velocity, horizontal left eye velocity, and horizontal right eye velocity, respectively. Saccade onset was considered to be the time that the vectorial eye velocity exceeded 50°/s and acceleration exceeded 10,000°/s². Saccade offset was defined as the first
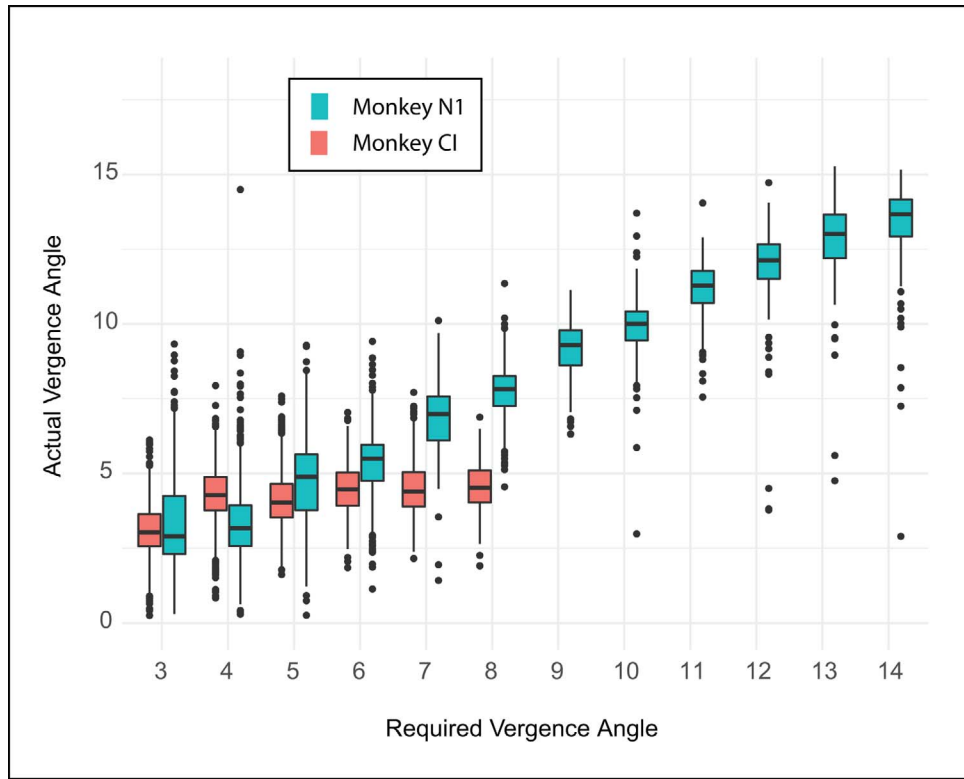
FIGURE 4. Comparison of observed and ideal vergence angles for various target distances during performance of the saccade-vergence task. Box plots show medians, with the boxes covering the 25th to 75th percentiles. The whiskers extend to 1.5× the height of the box, or to the most extreme value if there are no data points outside of this range. Outliers are plotted as individual points. In the interest of clarity, data are offset slightly along the *x*-axis. For the normal monkey (*cyan*) the observed vergence angle was typically close to the ideal vergence angle for all target distances. For monkey CI (*magenta*) the observed vergence angle reached a plateau of <5° convergence, even when the task required 8° convergence. It is important to note, however, that he was occasionally able to achieve vergence angles of ~7°. When the required vergence angle was >8°, monkey CI was unable to obtain the reward and quickly became frustrated and quit working. For this reason, the figure shows no data for this animal for panels with required vergence angles of 9° to 14°. Data are shown for the normal monkey (*cyan*) for this range, however, merely to demonstrate that he was able to perform the task correctly over a much larger range of required vergence angles.

point in time at which either of two criteria were met: (1) vectorial eye velocity fell below 50°/s or (2) vectorial eye velocity fell below 100°/s and the acceleration fell below 10,000°/s². Previous studies have reported that this algorithm successfully excludes large postsaccadic drifts that result in late reaccelerations of the eye (i.e., before the velocity dips below 50°/s) in monkeys with strabismus.[9,10]

Saccade latency was computed as the difference (in ms) between the time of the target step and the onset of the saccade. To assess whether saccade amplitudes in this animal were normal, we computed the saccade gain as follows:

$$Gain_{Saccade} = \frac{Amp_{Actual}}{Amp_{Ideal}}$$

For the near fixation task, we identified fixation periods that met the following criteria: (1) initial vergence angle of ≥10°, (2) fixation duration was at least 500 ms, (3) there were no detectable saccades, and (4) the monkey was looking in the direction of the checkerboard stimulus. Each fixation period began 100 ms after the last saccade and ended 10 ms before the next one. $Drift_{Verg}$ was defined as the change in vergence angle between these two time points. Negative values of $Drift_{Verg}$ indicate that the eyes diverged.

The tangent screen effect is well known in oculomotor research; the center and edges of a flat display screen are not equidistant from the eyes. Due to the small interpupillary distance in rhesus monkeys (typically 25–35 mm), this has little effect on the vergence angle when the screen is at far. When

the display screen is very close to the eyes, however, the tangent screen effect can no longer be ignored because a given change in target distance has a greater effect on the required vergence angle at near than at far. In the present case, the center of the full-field checkerboard pattern was 10 cm from the eyes, but the edges were approximately 12.2 cm away. The ideal vergence angle is the vergence angle that would result in perfect fusion of the visual target. It increases in a nonlinear fashion with the vectorial distance of the current gaze position, $Eccentricity_{Pre}$, from straight ahead. $Eccentricity_{Pre}$ (angle A, in Fig. 2A) was expressed in degrees and was computed using Equation 1:

$$Eccentricity_{Pre} = \sqrt{HorEcc^2 + VertEcc^2} \qquad (1)$$

Referring to Figure 2A, we can then compute angle B using Equation 2:

$$B = 180 - 90 - Eccentricity_{Pre} \qquad (2)$$

We can then use the Law of Sines (Equation 3) to determine the distance, D (in cm), from the cyclopean eye to the screen for the current gaze direction:

$$\frac{D}{\sin(90)} = \frac{10}{\sin(B)} \qquad (3)$$

Solving for D then gives the information necessary to compute the ideal vergence angle, based on the animal's interpupillary distance (Equation 4):
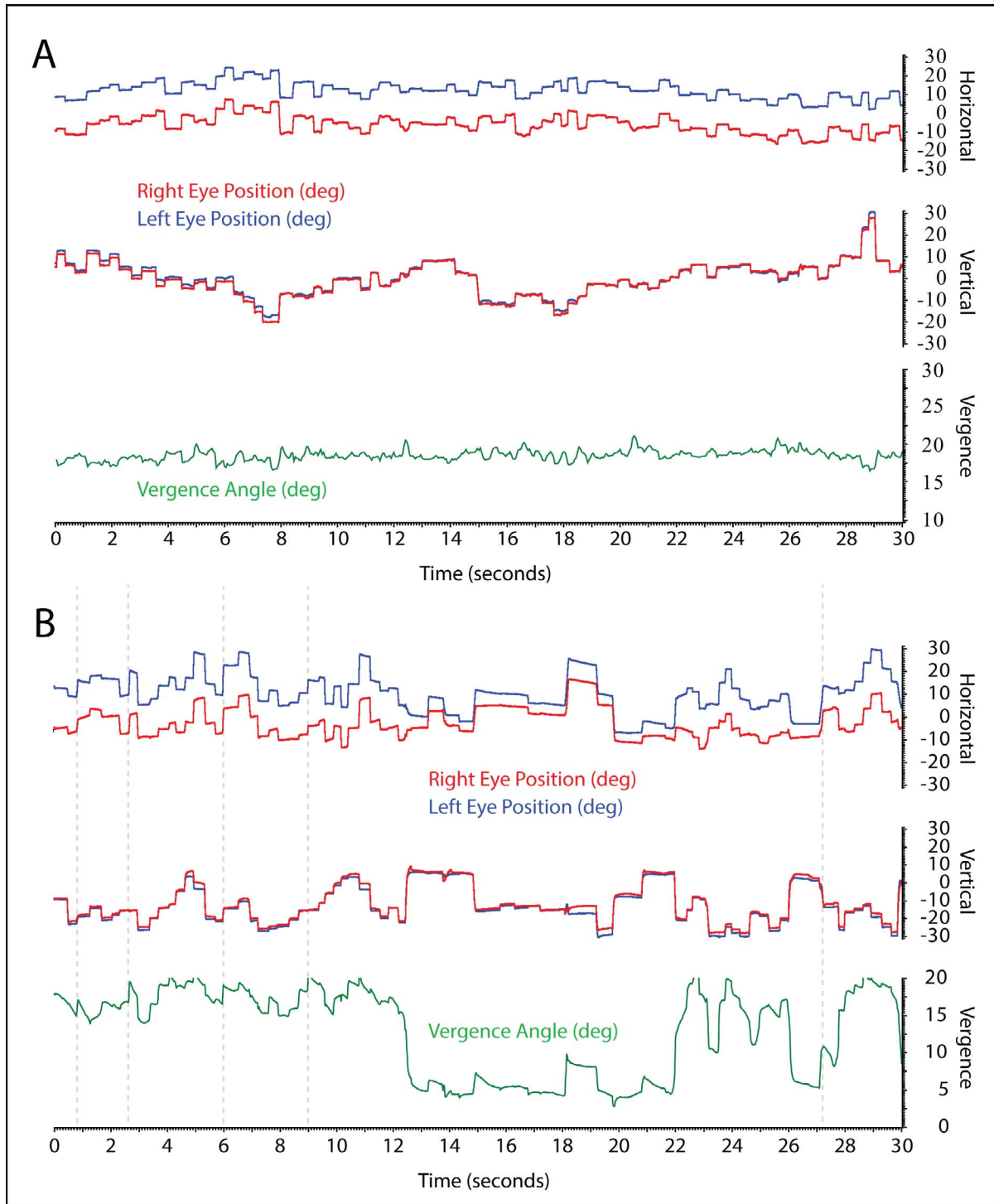
FIGURE 5. Thirty seconds of raw data during performance of the near fixation task. For the normal monkey (**A**), the vergence angle was fairly stable, even while the animal made voluntary saccades to visually explore the screen. In contrast, monkey CI (**B**) often failed to achieve, or maintain, the appropriate convergence. Converging saccades for this animal were typically followed by a slow divergence drift (several clear examples are identified by *vertical dashed lines*).

$$V_{ideal} = 2 * arctan \frac{I_{half}}{D} \qquad (4)$$

where I_{half} is half of the monkey's interpupillary distance (see Fig. 2B) and V_{ideal} is the ideal vergence angle for the current gaze direction. The difference between V_{ideal} before and after a saccade (post – pre) gives the ideal change in vergence angle for a gaze shift between any two points on the tangent screen

(ΔV_{ideal}). For each period of steady fixation, vergence error (V_{error}) was computed by subtracting V_{ideal} from the observed vergence angle. Similarly, for each saccade, ΔV_{ideal} was subtracted from the actual change in vergence angle to obtain V_{error}.

T-tests were used for a variety of comparisons (described in the relevant subsections in Results). Accordingly, the Bonfer-
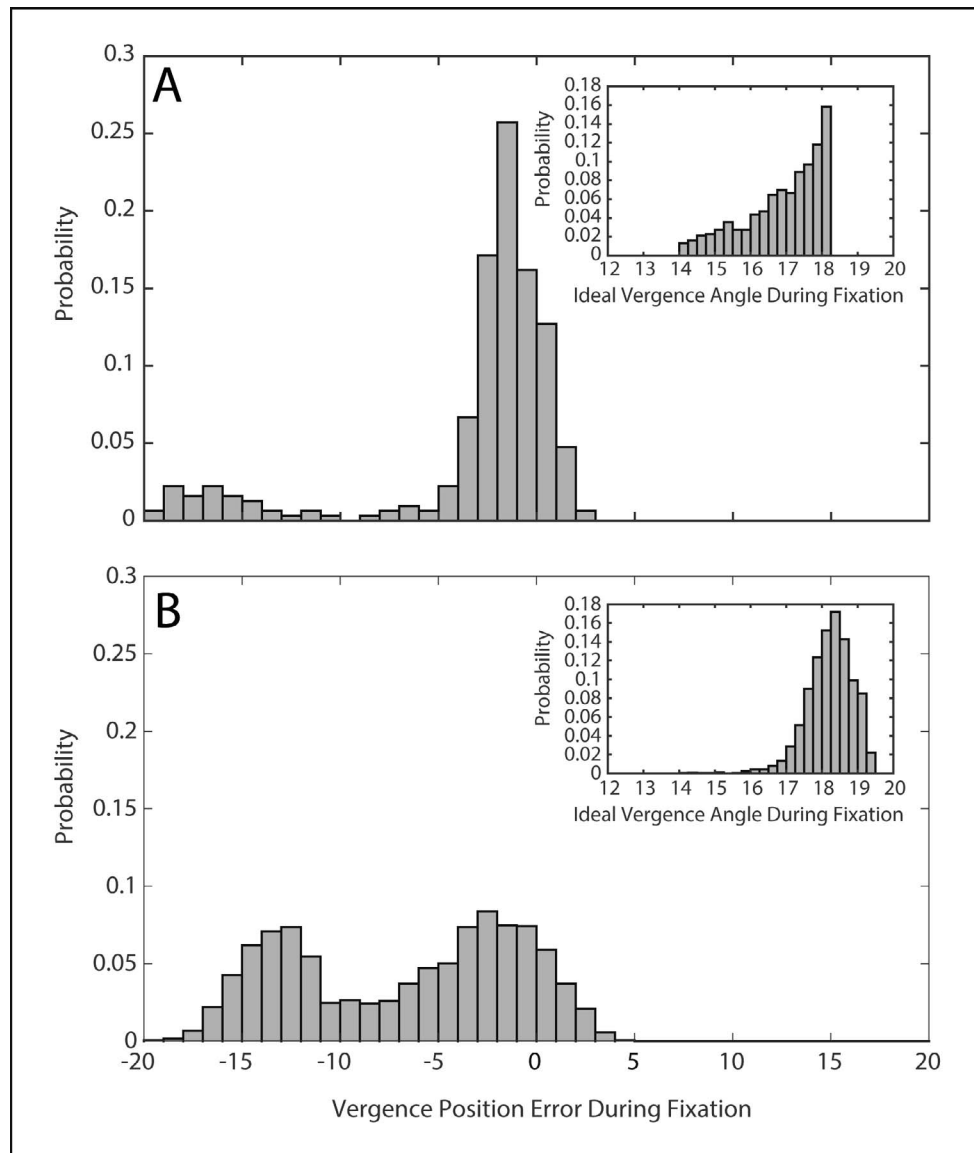
Figure 6. Distributions of vergence position error for a normal monkey (**A**) and monkey CI (**B**). Negative numbers indicate insufficient convergence. *Insets* show the distributions of ideal vergence angles (estimated using equation 4, see Methods) for both monkeys. The distributions differ for the two monkeys because the interpupillary distances were not the same for the two animals and because they tended to fixate different parts of the screen. Although both monkeys sometimes failed to achieve the appropriate convergence, the normal animal shows a large peak near a vergence position error of 0; by contrast, the distribution of vergence position error for monkey CI shows a large second peak near 12° to 13°.

roni correction was used to adjust the significance level, which was set to 0.0045.

RESULTS

Behavior

Target Step Saccade Task. Like other monkeys we have worked with, monkey CI1 quickly attained proficiency at the target step saccade task. Our saccade detection algorithm identified 872 target-directed saccades from monkey CI1 and 2426 from monkey N1. No significant difference was found between the mean saccade gains for monkey CI (1.01) and monkey N1 (1.00) (two-tailed t-test, $P = 0.90$). However, the mean saccade latency was significantly longer for monkey CI (279 ms), compared to monkey N1 (249 ms) (two-tailed t-test, $P < 0.001$).

Saccade-Vergence Array Behavior. Monkeys that are already proficient at the target step task typically learn the saccade-vergence task very quickly. Most are able to correctly fixate any of the 60 targets by the end of the first or second day. By the end of the first day, monkey CI1 was able to direct both eyes to any target that required ≤5° of convergence. A consistent exophoria was observed for any target that required ≥6° of convergence. The monkey showed no further improvement in the near point, even after more than a month of daily training. After this initial training period was over, we rarely asked this animal to converge by more than 8° because he would become frustrated by his inability to obtain the reward.

Figure 3 shows example raw data over a period of nearly two minutes. The normal animal had no difficulty converging by >12°, whenever the task required it (panel A). Monkey CI1 clearly understood the task and was able to bring both eyes to
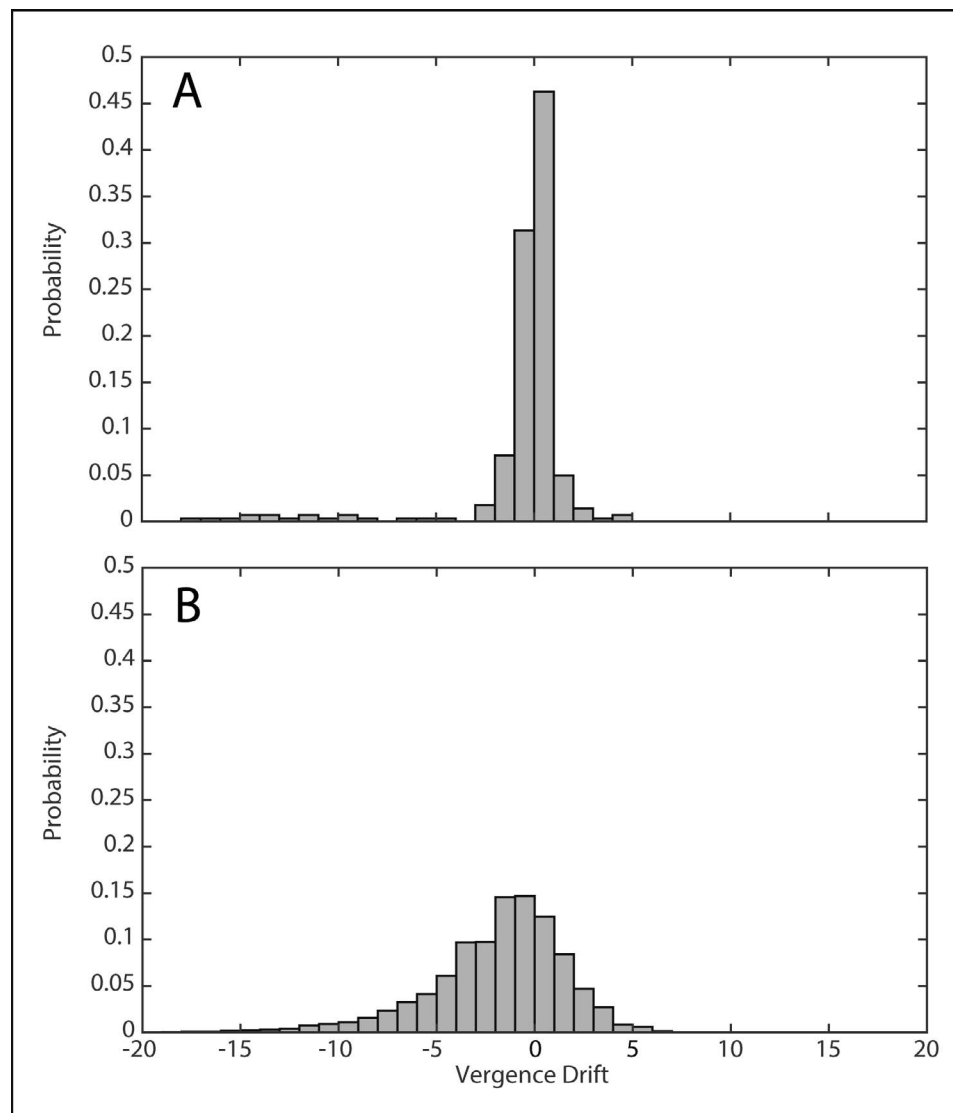
FIGURE 7. Distributions of vergence drift during attempted fixation of the checkerboard pattern in the near fixation task for a normal monkey (**A**) and monkey CI (**B**). For the normal monkey, vergence drift rarely exceeded ~1°. Even though monkey CI typically underconverged (see Fig. 6), vergence drift was typically negative, which would usually be the wrong direction.

the target when the required vergence angle did not exceed 4° (panel B). This animal responded to step changes in target distance by making vergence eye movements that were typically in the appropriate direction. When the target stepped from far to a distance requiring a vergence angle of >5°, however, the monkey consistently underconverged. This resulted in an exophoria. When the target was near, he usually fixated the target with the left eye while the right eye remained to the right of the target. It was not uncommon, however, for the animal to switch and fixate with the right eye, typically for a few seconds at a time. It is also worth noting that this monkey was sometimes able to transiently converge to 6° when required by the task but had difficulty maintaining this vergence angle.

Figure 4 compares the distributions of observed vergence angles, for each target distance, for monkeys N1 and CI1. For the normal animal, vergence angle steadily increased as target distance decreased. For monkey CI1, vergence angle was higher when the required vergence angle was 4° than when it was 3°. As the required vergence angle continued to increase, however, the observed vergence angle reached a plateau of

approximately 4.5° (5°–8° bins). Mean vergence angle differed significantly for the two monkeys for all bins for which data were available for monkey CI1 (two-tailed *t*-tests, $P < 0.00001$ for all comparisons).

Fixation of a Full Field Near Target. Although most monkeys have no difficulty with the saccade-vergence task, we hypothesized that a plus-shaped target subtending only 1° of visual angle might provide insufficient disparity and accommodative cues for monkey CI1. With this possibility in mind, we wondered whether a full-field visual stimulus at near might provide more robust cues that would help the animal to achieve an appropriate convergence. In addition, we wanted to present the animal with a stimulus that might be loosely analogous to what a human child experiences during reading.

Figure 5 shows 30 seconds of raw data from the near fixation task from monkeys N2 (panel A) and CI1 (panel B). For the normal animal, the vergence angle is fairly stable while the animal makes saccades to various locations. Although monkey CI1 was often able to achieve vergence angles of 15° or more, he clearly had difficulty maintaining convergence. Between ~12 and 22 seconds, the vergence angle is only ~3° to 8° even
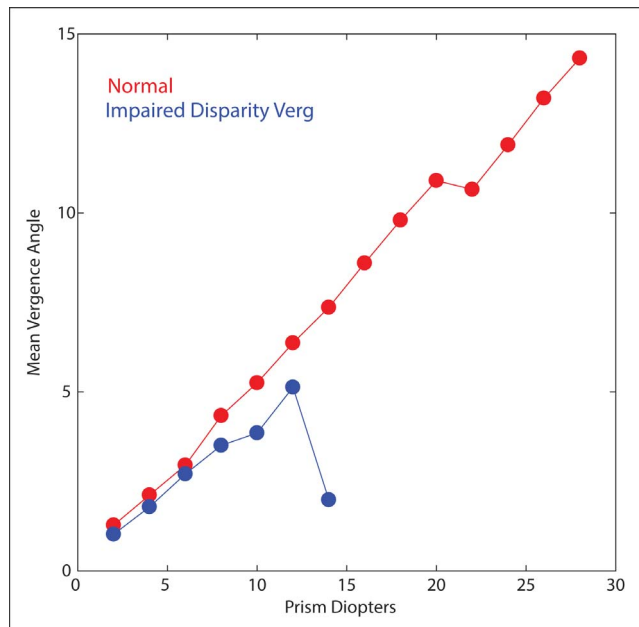
FIGURE 8. Results of Risley Prism testing for a normal monkey (*red*) and monkey CI (*blue*). Note that monkey CI's break-point during prism testing was quite similar to what we observed for this animal for other vergence tasks.

though the animal's gaze remains within ∼5° to 20° of the center of the stimulus pattern. Between 0 and 12 seconds, he is able to maintain convergence, but a close examination of the vergence angle trace during this period shows a recurring pattern of converging saccades followed by a slow divergence during the ensuing fixation period (see vertical dashed lines). This pattern was common across all data sets.

In all, 2357 fixation periods met the inclusion criteria for further analysis (see Methods) for monkey N2 and 2994 for monkey CI1. We measured the interpupillary distances of both monkeys to be approximately 34 mm. Using the equations described in the Methods section, we estimated that a saccade from the center of the screen to the edge should be associated with approximately 4° divergence. Conversely, saccades from the edge to the center should be associated with ∼4° convergence. In practice, however, these extreme saccades were rare because both animals preferentially chose to fixate locations closer to the center of the stimulus pattern; ΔV_{ideal} was almost always between −2 and 2. Monkey CI1, in particular, almost never chose fixation points near the edge of the screen (Fig. 6, insets).

Figure 6 shows the distribution of V_{error}. Negative values indicate that the convergence was less than ideal (V_{ideal}) for the current gaze position. Both monkeys sometimes failed to converge but this was uncommon for the normal animal and quite common for monkey CI1. It is clear from this figure that monkey CI1 was sometimes able to converge appropriately, but it was far more common for this animal to underconverge. For 427 fixations, the absolute value of V_{error} was less than 1°. For 1461 fixations, V_{error} was more negative than −5°, indicating that the animal underconverged by at least 5°. The mean value of V_{error} was significantly smaller for monkey CI1, compared to monkey N2 (two tailed *t*-test, $P < 0.00001$).

To analyze the vergence drift during fixation, we only considered fixations that were at least 500 ms in duration (monkey CI1, $n = 2315$; monkey N2, $n = 618$). Figure 7 shows the distribution of $Drift_{Verg}$ values across this data set. For monkey N2, the absolute value of $Drift_{Verg}$ was less than 1° for

479 fixations (78%), indicating a stable vergence angle. For monkey CI1, the absolute value of $Drift_{Verg}$ was less than 1° for 628/2315 of fixations (27%). The eyes diverged by at least 1° during 1283 fixation periods (55.4%) and by at least 5° in 356 (15.4%). The eyes converged by 1° or more for 401 fixations (17.3%). The tendency for monkey CI1's eyes to diverge during fixation was particularly noteworthy, given the fact that this animal was usually underconverged (Fig. 6), which means that the vergence angle often drifted in the wrong direction. Mean $Drift_{Verg}$ differed significantly for the two monkeys (two-tailed *t*-test, $P < 0.00001$).

Risley Prism Testing. To more directly assess monkey CI1's disparity vergence, we tested the animal using a Risley Prism and compared the results to those obtained from monkey N1. Figure 8 shows the results of this testing. For monkey N1, vergence angle increased as the prism power increased, up to 28 prism diopters and nearly 15° convergence. For monkey CI1, the results were very similar to those obtained from the normal monkey, up to 12 prism diopters, which resulted in 5° convergence. At 14 prism diopters, however, the animal was no longer able to converge (<2°). The test was repeated on a second day, with very similar results. Note that the maximum convergence observed for this animal during Risley prism testing was very similar to the maximum that this animal was able to achieve in the saccade-vergence task.

Smooth Vergence Tracking of Target Moving in Depth. In the saccade-vergence array, target size scaled with distance so that all targets would subtend the same visual angle. When a target is approaching the viewer, additional depth cues become available, such as looming. We wondered whether changes in the apparent size of the target would help monkey CI1 to be more successful during a smooth vergence tracking task. First, we consider the behavior of a normal monkey during the performance of this task. Figure 9A shows three cycles of vergence pursuit (0.1 Hz) from monkey N1, performed in darkness, with only the red fixation cross visible. As noted in the Methods section, a given change in target distance has a greater effect on the required vergence angle at near than at far. For this reason, even though the target motion followed a triangle wave pattern, the ideal vergence position did not. Perfect performance on this task requires a continuous increase in convergence velocity as the distance from the eyes decreases and a continuous decrease in divergence velocity as the target recedes. In addition, the vergence position consistently falls behind when the target reverses direction. This necessitates a "catch-up" period, during which the actual vergence velocity exceeds the "ideal" vergence velocity. The normal monkey was able to achieve this with some consistency. Panel B shows three cycles of vergence pursuit from monkey CI1, under the same conditions (i.e., 0.1 Hz, when the animal could see only the red fixation cross). Although the target was moving slowly, the monkey was unable to maintain pursuit, either in approach or recession, but sometimes did converge slightly when the target was at near. The maximum vergence angle was 5° to 6°, very similar to what was observed for the other tasks. When monkey CI1 performed the smooth vergence tracking task in a lighted room, with the red fixation cross surrounded by a random checkerboard pattern, he was more successful. Figure 10 shows three cycles of vergence pursuit under these conditions. The monkey was able to achieve the maximum convergence required by the task, and the animal's performance was not dramatically different from what we observed for normal monkeys performing the smooth vergence tracking task in darkness, without the checkerboard pattern (compare Fig. 10 to Fig. 9A).
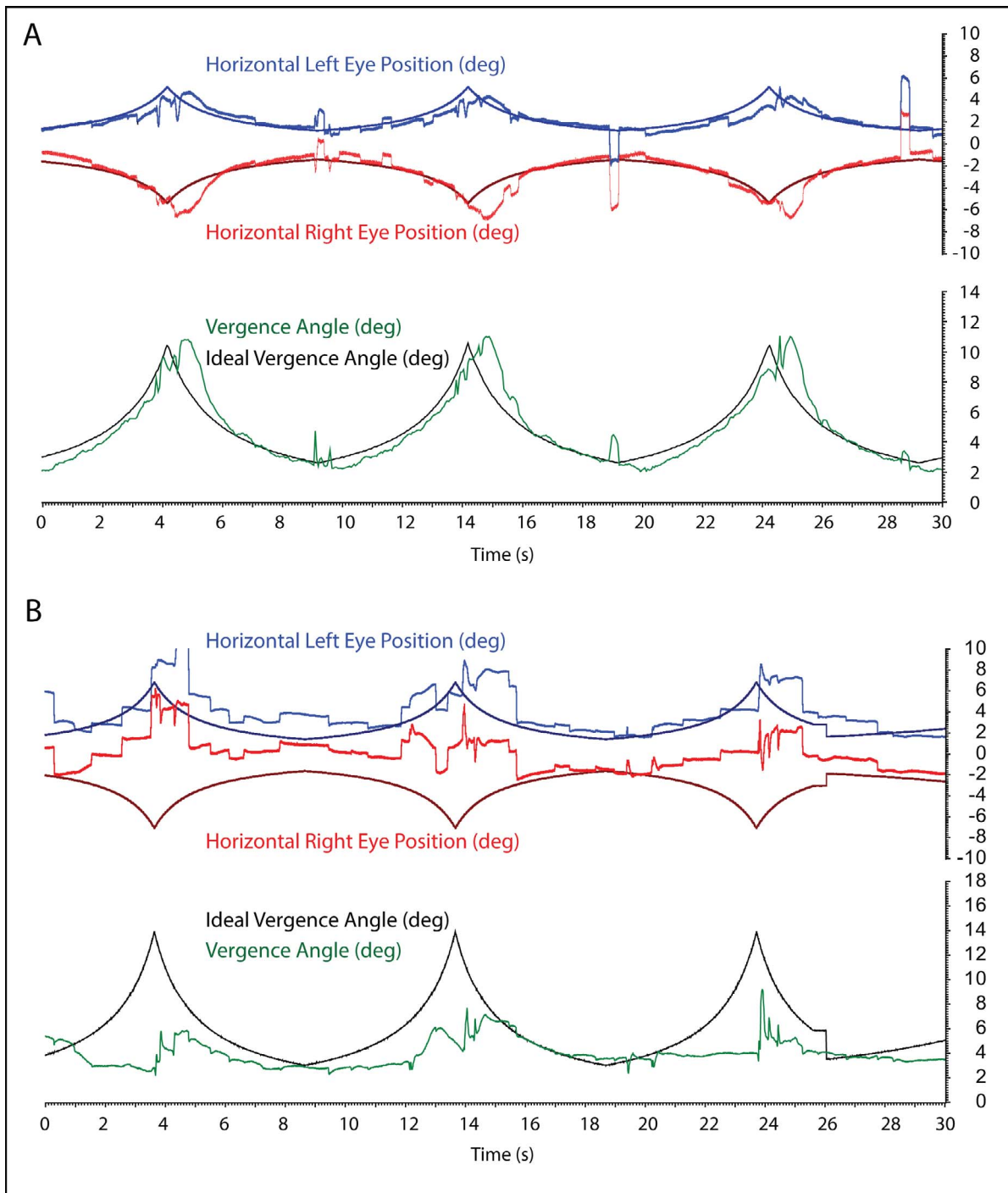
FIGURE 9. Thirty seconds of raw data during performance of the smooth vergence tracking task for a normal monkey (**A**) and monkey CI (**B**). In both cases, the red visual target was presented in darkness, without a large-field background. Once again, monkey CI was typically unable to converge more than ~5°, even when target motion was predictable, and depth perception should have been aided by an increase in the apparent size of the target.

Despite the animal's difficulties with the near fixation task, it is clear that he was much better at converging when the target was surrounded by a full-field random checkerboard pattern, which was a much more robust disparity and accommodative stimulus. We wondered which of these depth cues the monkey was relying on to achieve convergence angles that far exceeded what he was able to attain during the saccade-vergence task. If the animal is relying entirely on monocular depth cues, such as looming and accommodative

blur, then he should still be able to converge when one eye is patched. Conversely, if he is making use of a combination of binocular and monocular depth cues, then performance should degrade. Figure 11 shows three cycles of vergence pursuit with the right eye patched, with the room illuminated and the target surrounded by the random checkerboard pattern. Under these conditions, the severe deficits in vergence pursuit reappeared.

Figure 12A compares the actual and ideal vergence velocity traces for several cycles of pursuit in depth, conducted in
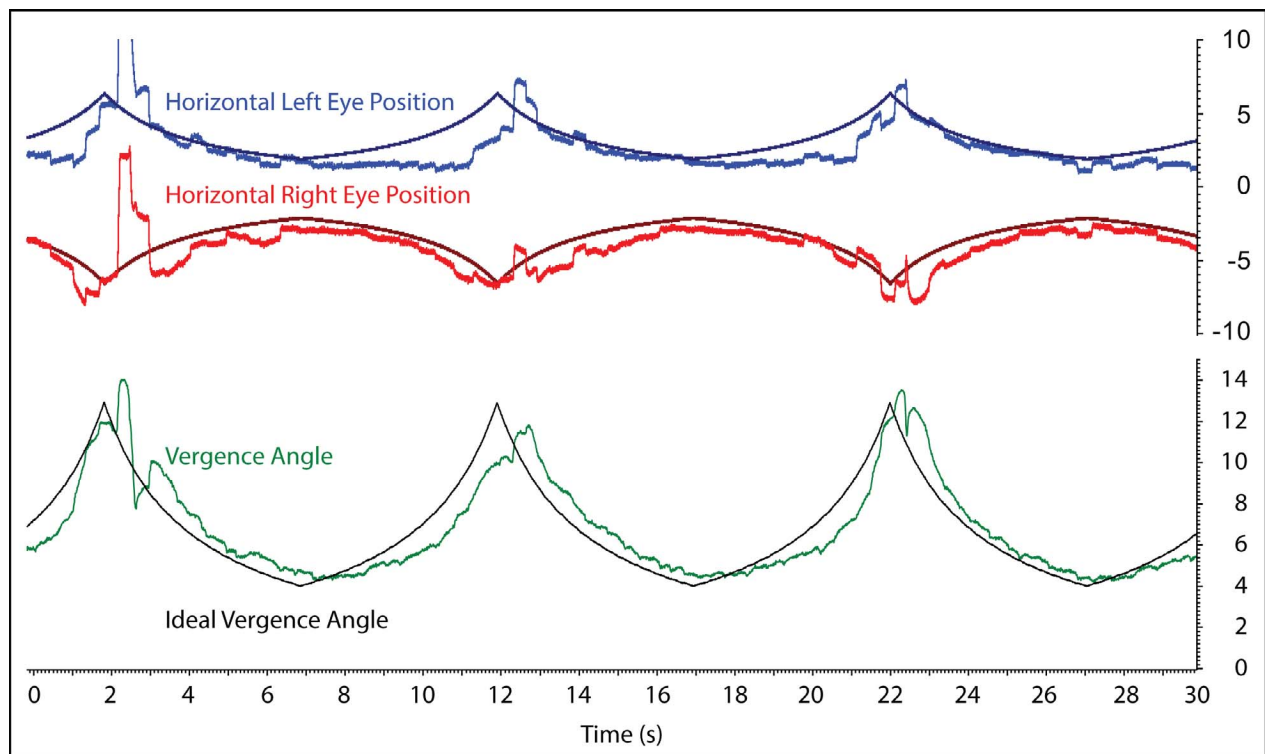
FIGURE 10. Thirty seconds of raw data during performance of the smooth vergence tracking task for monkey CI, when the room lights were on and the visual target was surrounded by a large-field checkerboard pattern. Note that the inclusion of disparity and/or accommodative information from across the visual field enabled the animal to achieve a fairly normal performance.

darkness. The normal animal was able to match the ideal vergence velocity almost perfectly throughout the cycle (top) but monkey CI1 was able to do so only for short periods of time (arrows indicate several examples of this). For this latter animal, much of the change in vergence angle was achieved by making disjunctive saccades, which gives the vergence velocity trace a "choppy" appearance (other examples of this can be seen in Fig. 9). Panels B through D plot the mean vergence angle as a function of ideal vergence angle for all cycles of pursuit-in-depth at two frequencies (0.1 Hz and 0.2 Hz). For the normal monkey (panel B), actual vergence angle approximately matched the ideal vergence angle during both approach and recession at 0.1 Hz. This was also true for convergence at 0.2 Hz, but at this faster speed, the vergence position fell behind during the first several seconds of the diverging phase before catching up around the middle of the cycle. When monkey CI1 attempted the same task under identical conditions, the mean vergence angle was consistently lower than the ideal vergence angle, and this vergence position error worsened whenever the target was near (panel C). When monkey CI1 performed the task in a lighted room under binocular viewing conditions, with the target surrounded by the random checkerboard pattern, the mean vergence angle approximately matched the ideal vergence angle, even when the target was near (panel D).

Although the geometric relationships between ideal vergence angle and the distance of an object approaching at constant velocity are complex, Figure 12 indicates that the relationship between actual and ideal vergence angle is approximately linear. With this in mind, the above observations were quantified by performing linear fits on this relationship, using Matlab's curve fit tool. Comparisons between slopes or intercepts for linear fits were taken to be significantly different if the 95% confidence bounds for the two

fits did not overlap. The results of this analysis are shown in the Table. The slope was significantly lower for monkey CI1, compared to monkey N1, for all conditions except when the vergence-impaired monkey was viewing the target in light, with a large-field background, under binocular viewing conditions. For monkey CI1, the slope was also significantly larger for both monocular+viewing+background conditions, compared to binocular viewing in darkness, without the large field background.

DISCUSSION

In this study, we report behavioral data from a rhesus monkey with a naturally occurring impairment of vergence eye movements. For normal monkeys, a small (subtending 1° of visual angle), red, plus-shaped LED provides sufficient disparity and accommodative cues for robust vergence behavior in an otherwise dark room.[11] Similarly, the present data show that a target of the same shape, color, and physical size elicits robust, accurate smooth vergence pursuit when it moves in depth. Under identical conditions, however, monkey CI1 was unable to achieve the convergence required by these tasks, even after months of training. From the Risley Prism testing, it is clear that this animal had a significant impairment of disparity vergence. Despite this, the animal was able to successfully perform a smooth vergence pursuit task in a lighted room, when the target was surrounded by a large-field random checkerboard pattern. This indicates that monkey CI1 relies on monocular depth cues, presumably including accommodative blur, to achieve appropriate convergence. However, the vergence pursuit deficits returned when one eye was patched, and the monkey was unable to sustain the required vergence angle on the near fixation task, even when the random checkerboard pattern was available. This pattern of results
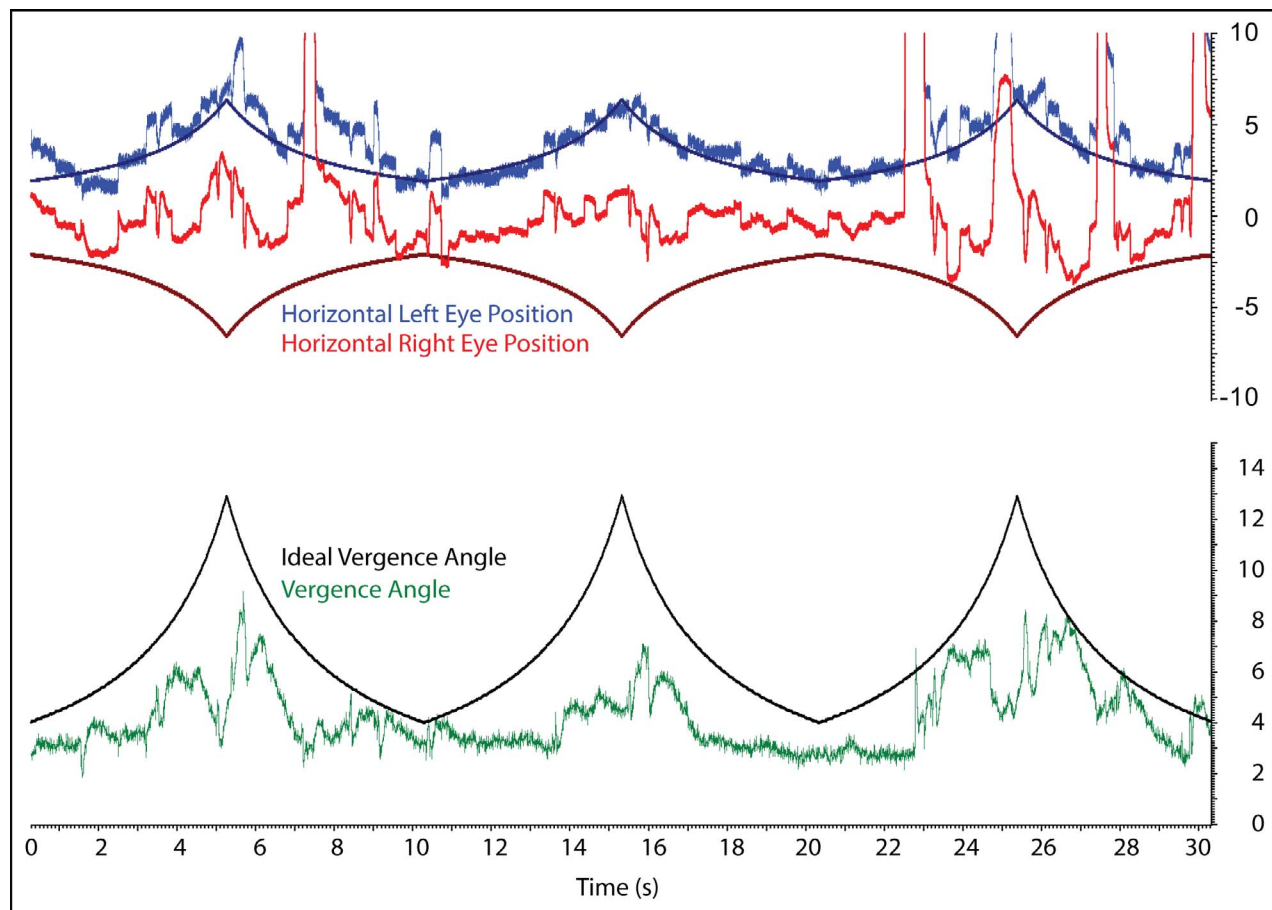
Figure 11. Thirty seconds of raw data during performance of the smooth vergence tracking task for monkey CI, under monocular viewing conditions, when the room lights were on and the visual target was surrounded by a large-field checkerboard pattern. Note that the severe vergence deficits reappeared when binocular depth cues were unavailable. Thus, although binocular disparity seems to be insufficient for this monkey to achieve appropriate convergence (see Fig. 8), it is, apparently, necessary.

strongly suggests that, although binocular depth cues were insufficient to achieve approximately normal convergence, they were necessary. Interestingly, the animal had more difficulty with the near fixation task than the vergence pursuit task when the checkerboard pattern was visible. This suggests that the monkey was using depth cues related to target motion (i.e., looming and radial optic flow). These same cues would be available to human observers during appropriate conditions, which could improve performance.

Table. Y-intercepts (Y-int), Slopes, and Variance Accounted for (R^2) for Linear Fits to the Relationship Between Actual and Ideal Vergence Angle

Cell	Y-int	Slope	R^2
N1, binocular, darkness	0.69	0.89	0.46
CI1, binocular, darkness	2.97	0.18	0.11
CI1, binocular, with large-field background	−0.4	0.93	0.51
CI1, left eye patched, with large-field background	1.45	0.26	0.18
CI1, right eye patched, with large-field background	1.2	0.44	0.43

Monkey CI's vergence impairments closely resemble convergence insufficiency in human patients, in several important respects. For example, normal humans show an NPC (i.e., the minimum distance at which sensory fusion can be achieved) of 5 to 10 cm from the bridge of the nose. Normal monkeys can also show appropriate convergence for targets at a distance of 10 cm.[11] For human patients with convergence insufficiency, the NPC may be 20 to 30 cm.[1] In the present study, monkey CI also showed a severely abnormal NPC. Human patients with convergence insufficiency typically show an exodeviation that worsens as a visual target gets closer.[1,12–14] Monkey CI also showed this abnormality (see Figs. 3, 4, 8, and 9). When presented with a near target, monkey CI typically fixated with the left eye but occasionally made saccades that brought the right eye to the target (several examples of this can be seen in Fig. 3), suggesting that the animal may have experienced diplopia, as do human patients with convergence insufficiency.

Treatment of convergence insufficiency typically involves behavioral therapies that train the vergence system, such as pencil push-ups.[1,15,16] Our smooth vergence tracking task is somewhat similar to these exercises, but we did not observe any improvement in this animal, even after months of training. This might reflect a species difference, but it should be noted that vergence exercises do not always lead to a significant improvement in human patients.[15]
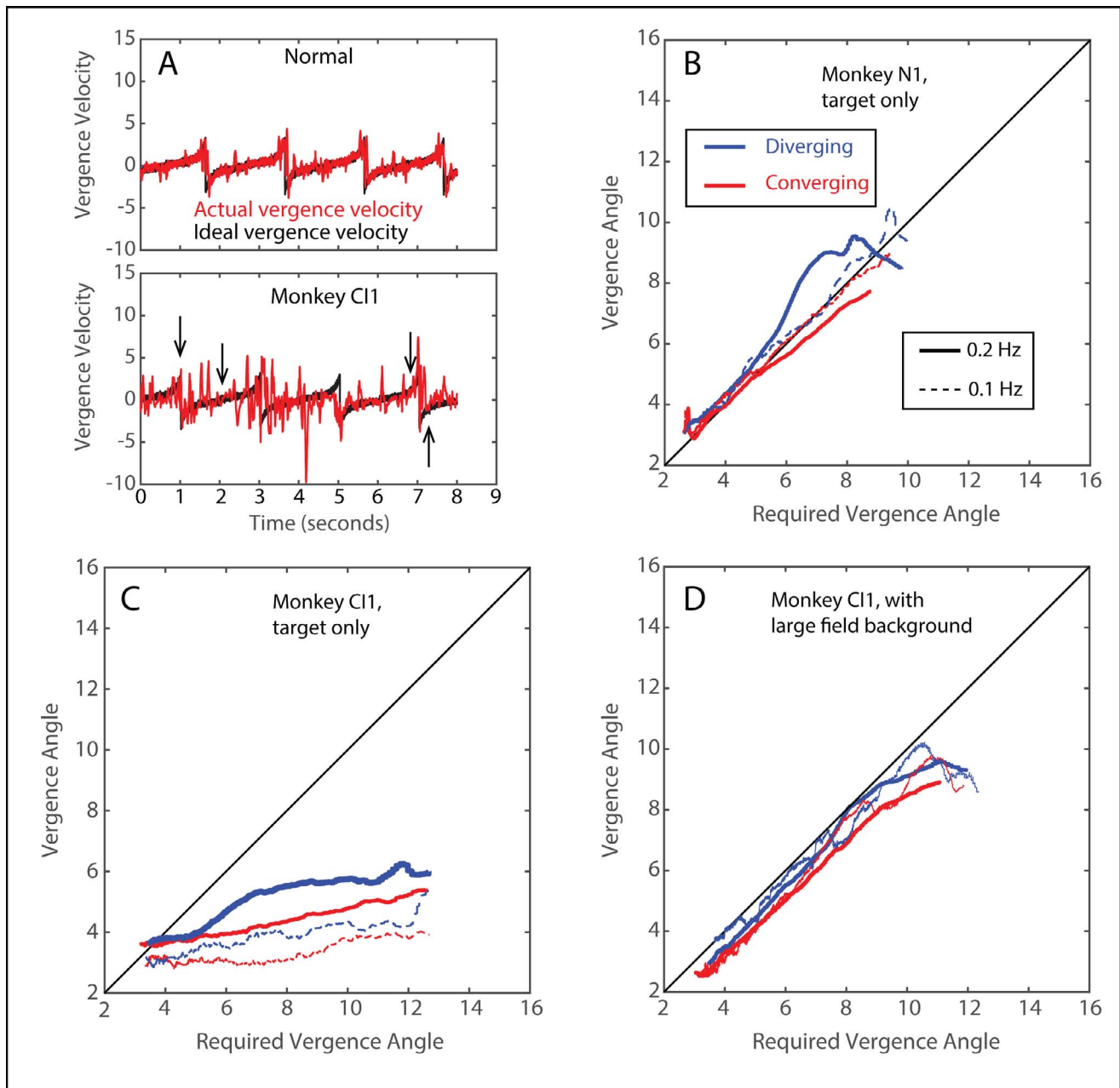
FIGURE 12. Comparison of results for different variations of the smooth vergence tracking task. When only the *red cross* was visible, the normal monkey was able to maintain the appropriate vergence velocity, during both approach and recession (panel **A**, *top*). Under the same conditions, monkey CI was sometimes able to transiently achieve the appropriate vergence velocity (*arrows*) but did not consistently maintain it. Under these conditions, the normal monkey's vergence angle was typically very close to ideal (**B**), but monkey CI underconverged (**C**). However, when performing this task in a lighted room, under binocular viewing conditions, with the target surrounded by a large-field checkerboard pattern, monkey CI was able to maintain an appropriate vergence angle throughout the task, during both convergence and divergence.

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