Atmospheric $P_{\text{CO}_2}$ Perturbations Associated with the Central Atlantic Magmatic Province

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The effects of a large igneous province on the concentration of atmospheric carbon dioxide ($P_{\text{CO}_2}$) are mostly unknown. In this study, we estimate $P_{\text{CO}_2}$ from stable isotopic values of pedogenic carbonates interbedded with volcanics of the Central Atlantic Magmatic Province (CAMP) in the Newark Basin, eastern North America. We find pre-CAMP $P_{\text{CO}_2}$ values of ~2000 parts per million (ppm), increasing to ~4400 ppm immediately after the first volcanic unit, followed by a steady decrease toward pre-eruptive levels over the subsequent 300 thousand years, a pattern that is repeated after the second and third flow units. We interpret each $P_{\text{CO}_2}$ increase as a direct response to magmatic activity (primary outgassing or contact metamorphism). The systematic decreases in $P_{\text{CO}_2}$ after each magmatic episode probably reflect consumption of atmospheric $CO_2$ by weathering of silicates, stimulated by fresh CAMP volcanics.

Large igneous provinces (LIPs) are geologically rapid episodes of extensive volcanicism, often flooding vast oceanic or continental regions with several million cubic kilometers of lava (1). In particular, continental flood basalts have the potential to directly perturb Earth’s climate system through the emission of gasses to the atmosphere: most notably, $SO_2$ and $CO_2$, which together may result in an immediate (1- to 10-year) cooling (2, 3), followed by a longer-term (10^-2- to 10^-3-year) warming (4). Of these, only $CO_2$ has the potential to influence climate on both short and long time scales because of its relatively long atmospheric residence time and effectiveness as a greenhouse gas, leading some to conclude that $CO_2$ is the primary driver of Phanerozoic climate (5).

If the concentration of atmospheric $CO_2$ exerted an influence on climate over such broad time scales, what are the effects of a LIP on this essential parameter of the carbon cycle? Although the potential radiative effects of LIP $CO_2$ degassing on the million-year scale have been considered inconsequential (6, 7), shorter (10^-2- to 10^-1-year)-time scale reconstructions of atmospheric partial pressure of $CO_2$ ($P_{\text{CO}_2}$) before and after LIP eruptions have not been systematically determined because of inadequate chronostratigraphic resolution in most settings (8, 9). Consequently, the direct $P_{\text{CO}_2}$ effect of a LIP remains untested empirically.

Intriguingly, LIP volcanicism is often temporally associated with mass extinction events throughout Earth’s history (10). The three largest continental LIPs of the Phanerozoic are the Siberian Traps, the Central Atlantic Magmatic Province (CAMP), and the Deccan Traps, each of which is linked to one of the “Big 5” Phanerozoic mass extinctions [the end-Permian, end-Triassic, and the Cretaceous–Paleogene events, respectively] (11, 12). Though attempts have been made to estimate the gaseous emissions attributable to the Deccan (6, 13, 14) and Siberian (15, 16) traps, it is difficult to demonstrate causality because the uncertainties in correlating these $P_{\text{CO}_2}$ estimates from afar to the volcanic stratigraphy itself are usually no better than the turnover time of an atmospheric $P_{\text{CO}_2}$ perturbation (17). Of these, only the CAMP is sequenced in high-resolution, temporally continuous sediments that contain paleosols appropriate for estimating $P_{\text{CO}_2}$ and have a well-established chronology (18, 19) and extinction level.

Extrusives from the CAMP (20) are preserved in direct stratigraphic succession with cyclic continental sediments in the Newark Basin of eastern North America (Fig. 1). Milankovitch cyclostratigraphy of the primarily lacustrine sediments interbedded within the CAMP extrusives have yielded precise age control (to the level of orbital precession) and an estimated total volcanic duration of ~600 ± 20 thousand years (ky) (21, 22). In this same Newark Basin section, palynofloral evidence of the end-Triassic extinction (ETE) is found stratigraphically just below the first of the CAMP volcanics, preceding the magmatism by ~20 ky (23), see (24) for review]. Also interspersed throughout these sediments, and often forming from CAMP lava flows themselves, are pedogenic carbonate-bearing paleosols (Fig. 2, A and B), which can be used to estimate ancient atmospheric $P_{\text{CO}_2}$ (25). Thus, the Newark stratigraphy is ideally situated to directly test the $P_{\text{CO}_2}$ effect of a LIP.

Previous attempts at reconstructing the $P_{\text{CO}_2}$ effect associated with CAMP extrusives had very sparse sampling resolution (26) or had to rely on imprecise long-distance correlation (8, 9).

We use $\delta^{13}C$ measurements of pedogenic carbonate nodules from paleosols stratigraphically distributed before and after each extrusive unit to generate a high-resolution $P_{\text{CO}_2}$ record through the Newark Basin CAMP sequence (Fig. 1). The extrusion of ~2 to 4 × 10^6 km^3 of volcanics (27, 28) in less than 1 million years (My) implies a measurable effect on atmospheric $P_{\text{CO}_2}$, which our temporal resolution should allow us to detect. According to the model of Dessert et al. (17) scaled to the Deccan Traps, the transient increase in $P_{\text{CO}_2}$ is on the time scale of the eruptions, after which continental silicate weathering should lower $P_{\text{CO}_2}$ to pre-eruption levels in ~1 My.

**Estimating $P_{\text{CO}_2}$ from pedogenic carbonates.** Organic and inorganic carbon isotope measurements on paleosols from outcrop—and from multiple, stratigraphically overlapping cores taken by the Army Corps of Engineers (ACE) through the extrusive interval (fig. S1) (29)—are used as inputs into the diffusion model of Cerling (30)

$$C_s = S(z) \delta_s - 1.0044 \delta_s - 4.4 \delta_s - \delta_s$$ (1)

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**Fig. 1.** (A) Stratigraphy and lithology (22, 34, 41) of the upper Newark Basin stratigraphic section, based on assembly of a series of short cores taken by the ACE covering the extrusive interval in high resolution (49), with substantial overlap both internally and with the Newark Basin Coring Project (NBCP) Martinsville core (19, 22) and outcrop. Note that the ETE event (red) is several meters below the equivalent of the Orange Mountain Basalt (OMB, the first flow unit) in the Jacksonwald section of the Newark Basin (24). Stratigraphic thickness is scaled arbitrarily from the base of the laterally extensive OMB. J, Jurassic; Tr, Triassic; UU through MM are stratigraphic members. (B) Profile-equilibrated mean $\delta^{13}C$ values of pedogenic carbonate in the Newark stratigraphic section. Error is ±SD of mean (Fig. 2 and table S1) (29). Circles, samples from core; squares, outcrop. PB, Pee Dee belemnite. (C) Measured $\delta^{13}C$ values of preserved soil organic matter from clay linings or as close to the paleosol surface as possible. (D) Results of the pedogenic carbonate paleobarometer based on the input variables from (B) and (C) at 25°C. The concentration of respired $CO_2$ in the soil (S[z]) was estimated to be 3000 ± 1000 ppm (error bars), corresponding to a plausible range for midproductivity tropical soils and probably encompassing the range of calculated atmospheric $P_{\text{CO}_2}$ values. Carbon-cycle perturbations are built into the model because the carbon isotopic ratio of the atmosphere ($\delta_s$) is calculated from the measured $\delta^{13}C_{\text{org}}$ by $\delta_s = \delta^{13}C_{\text{org}} + 18.67/L.10 (32)$, which assumes consistent fractionation by photosynthesis [see (29) and table S1 for numerical values].

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where $C_a$ is the concentration of atmospheric CO$_2$, $S(z)$ is the concentration of CO$_2$ due to respiration of soil organic matter, $\delta_z$ is the $\delta^{13}$C of soil CO$_2$, $\delta_a$ is the $\delta^{13}$C of soil-respired CO$_2$, and $\delta_s$ is the $\delta^{13}$C of atmospheric CO$_2$. All $\delta$ values are relative to Vienna Pee Dee belemnite (VPDB).

The temperature of calcite precipitation is set at 25°C, relating the carbon isotopic ratio of soil carbonate ($\delta_{cc}$) to $\delta_s$ (29). As an independent objective metric of soil applicability, multiple (three or more) down-profile $\delta_{cc}$ measurements were made on each paleosol to reproduce the
expected exponential decrease toward stabilization with depth (Fig. 2) (29, 31). Using the mean of these soil-equilibrated measurements ensures that the mixing between the atmospheric and soil-respired reservoirs is at equilibrium with respect to the diffusion model. The measured carbon isotopic ratio of soil organic matter \((\delta^{13}C_{\text{org}})\) is related directly to \(\delta_t\) (29). Carbon-cycle perturbations are built into the model because the carbon isotopic ratio of the atmosphere \((\delta_a)\) is calculated from the measured \(\delta^{13}C_{\text{org}}\) by assuming consistent fractionation by photosynthesis: 
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\delta_t = (\delta^{13}C_{\text{org}} + 18.67)/1.10 (32). \]
We use an \(\delta_t\) value of 3000 ± 1000 parts per million (ppm), appropriate for soils developed in a semi-arid climate with moderate productivity (30, 33).

Atmospheric \(P_{\text{CO}_2}\) estimates in superposition with CAMP basalt. Pedogenic carbonates from the uppermost Passaic Formation, deposited over (Fig. 1D). These estimates from over 500 m of terrigenous weathering in the Late Triassic.

The ~2000-ppm pre-CAMP \(P_{\text{CO}_2}\) baseline found in this study is not inconsistent (geographically and stratigraphically) dispersed pedogenic carbonate estimates from elsewhere in the Newark and Hartford stratigraphy (34). Model results of the pedogenic carbonate paleobarometer yield \(P_{\text{CO}_2}\) estimates with a mean of ~2000 ppm \([\delta_t = 3000 \text{ ppm}]\) in the pre-CAMP stratigraphy (Fig. 1D). These estimates from over 500 m of the uppermost Passaic Formation, deposited over ~2.5 My of the latest Triassic (18, 19), show internal consistency between outcrop and between cores and, with the tight stratigraphic resolution, suggest that there are no major \(\text{CO}_2\)-producing magmatic events before the observed Orange Mountain Basalt. This stable \(P_{\text{CO}_2}\) background is probably a measure of equilibrium continental silicate weathering in the Late Triassic.

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The carbon isotope value of pedogenic carbonate formed directly on top of the Orange Mountain Basalt (first flow unit) is enriched in \(^{13}\text{C}\) by 1 to 2‰ above the pre-CAMP background (Fig. 1B). This increase and similar increase above the Preakness and Hook Mountain Basalts (the second and third flow units, respectively) reflect the increased influence of the atmospheric reservoir on soil carbonate formed at depth. Stratigraphically, above each flow unit, the carbon isotope composition of soil organic matter decreases by ~0.5 to 1.0‰, followed by a general return of \(\delta^{13}C_{\text{org}}\) values to ~26‰, but with increased variability (Fig. 1C). The \(\delta^{13}C\) values of pedogenic carbonate and soil organic matter directly above the Preakness Basalt have particularly good reproducibility between several laterally equivalent individual cored sections, allowing confidence in these measurements. These soils formed on top of the Orange Mountain Basalt (Fig. 2B) show an increase in \(P_{\text{CO}_2}\) to 4400 ppm (Fig. 1D), which amounts to a doubling of \(P_{\text{CO}_2}\) above the pre-CAMP baseline. In every case, pedogenic carbonate samples of soils formed on the tops of the basaltic units yield \(P_{\text{CO}_2}\) estimates that are distinctly higher than the immediately pre-eruptive background levels (Fig. 1): 4200 ppm on top of the Preakness Basalt compared with 3000 ppm in the uppermost portion of the underlying Felvtone Formation, and 5000 ppm directly on the Hook Mountain Basalt compared with 2500 ppm in the uppermost portion of the underlying Towaco Formation. This pattern suggests that the volcanism associated with each lava-flow unit had a direct effect on atmospheric \(\text{CO}_2\) by ~2000 ppm and was virtually immediate [to within the resolution of orbital precession (~20 ky)].

Chronostratigraphic control of \(P_{\text{CO}_2}\) estimates. A previous low-resolution reconstruction from the Newark Supergroup (two localities over 10 My) suggested that relatively stable \(P_{\text{CO}_2}\) levels across the CAMP interval (26) and, when compared to our study, underscores the difficulty in attempting to capture a transient perturbation of the carbon system without adequate chronostratigraphic control (Fig. 3) (38, 39). The stratigraphic level of the McCoy Brook sample of Tanner et al. (26) from the Fundy Basin is not known precisely (40), and it is quite possible that the soil formed long enough after emplacement of the North Mountain Basalt (correlative to the Orange Mountain Basalt) (41) that the full \(P_{\text{CO}_2}\) increase was not recorded. As demonstrated by this study, capturing such a transient signal such superposition removes any stratigraphic uncertainty from these \(P_{\text{CO}_2}\) estimates with regard to the flow units themselves. (C) Down-soil \(\delta^{13}\text{C}\) profiles of pedogenic carbonates \((\delta_t)\) from representative paleosols in the Passaic, Felvtone, Towaco, and Boonton Formations used in this study (symbols encompass analytical error), compared with the \(\delta_t\) predicted by the diffusion model at atmospheric \(\text{CO}_2\) concentrations of 2000 and 4000 ppm (blue and pink lines, respectively) [after (37)]. For this exercise only, atmospheric \(\delta^{13}\text{CO}_2\) was set to ~6.5‰, and soil \(\delta^{13}\text{C}_{\text{org}}\) was set to ~26.5‰, with an exponential production function and characteristic depth of production at 15 cm [see (29) for description of other parameters]. For all \(P_{\text{CO}_2}\) estimates made in this study, the \(\delta^{13}\text{C}_{\text{org}}\) was measured directly and used as a model input. Soil carbonate above 20 cm in the profile was rare. Note that stabilization of measured \(\delta_t\) is often well below 50-cm soil depth. Using the mean of these depth-stabilized measurements ensures the mixing between the atmospheric and soil-respired reservoirs at equilibrium with respect to the diffusion model. Photographs of the soils used in (C), from samples NFPT26 and NTCL24, are shown in (A) and (B).
requirements <100-ky sampling resolution with respect to the volcanics. Other attempts to estimate $P_{CO_2}$ over this interval, most notably the approximations using stomatal densities of leaf fossils from end-Triassic event boundary sections in Greenland and Sweden (9), indicate a doubling to tripling of $P_{CO_2}$ from 800 to 2100 ppm (Fig. 3). These stomata-based estimates are substantially lower than those found here, but the stomata proxy is thought to underestimate $P_{CO_2}$ (42), in which case a reported doubling to tripling broadly agrees with our findings and is corroborated by other cuticular estimates (43).

If the increase in $P_{CO_2}$ after each major basaltic unit (Orange Mountain, Preakness, and Hook Mountain Basalts) can be ascribed to episodes of magmatic activity, which are likely to be very short (22), then the relatively high-resolution record of $P_{CO_2}$ taken as a whole seems to require just the three distinct episodes of volcanism. This does not necessarily imply that the local thicknesses of the CAMP volcanics in the Newark are representative of the global volume of basalt produced by each flow unit. For example, although the Newark and Hartford Basins show three distinct volcanic episodes in nearly identical chronostratigraphic sequence (41, 44), the thicknesses of the correlative flow units vary by a factor of 2. Nonetheless, the observed magnitude and singularity of the $P_{CO_2}$ response to each flow unit in the Newark Basin implies that the magmatic events that produced them were regionally extensive and voluminous, because atmospheric $CO_2$ is globally homogeneous on the circulation time of the atmosphere. Although the second episode of magmatism produced the thickest lava flow unit (Preakness Basalt) in the Newark Basin, there is only a relatively small corollary increase in $P_{CO_2}$. Interestingly, a middle flow unit equivalent to the Preakness Basalt is not present in the South Atlas region of Morocco, whereas the uppermost flow unit there (Recurrent Basalt) is stratigraphically and geochemically equivalent to the Hook Mountain Basalt in the Newark Basin (41). Although the Hook Mountain Basalt is locally thin in the Newark, the associated $P_{CO_2}$ increase is one of the largest recorded, implying that greater unrecorded volumes were erupted elsewhere. This body of evidence demonstrates the global applicability of the $P_{CO_2}$ findings reported here; together, they make a compelling case that what has been recorded in the Newark Basin is a reasonable representation of a global sequence of events.

To gauge the plausibility of a volcanic $CO_2$ source, we can compare the $CO_2$ efflux potential of the CAMP basalt volume to the effect observed in the Newark. Assuming a total CAMP volume of $2.4 \times 10^6$ km$^3$ (27) and a volcanic efflux of $1.4 \times 10^{10}$ kg of $CO_2$ per km$^3$ (7), we estimate a total $CO_2$ degassing potential of $3.36 \times 10^{16}$ kg $CO_2$. We focus on the lower volcanic unit (represented by the Orange Mountain Basalt in the Newark Basin), for which the pre-eruption background $P_{CO_2}$ is well established. That initial pulse of activity represents roughly one-third of the total CAMP volume and, therefore, could have produced $1.12 \times 10^{16}$ kg of $CO_2$ amounting to a ~1400-ppm increase in $P_{CO_2}$ (at $7.82 \times 10^{12}$ kg $CO_2$ per ppm). This instantaneous approximation is of the same order and within the error of our observed ~2000-ppm $P_{CO_2}$ increase after the first major episode of CAMP volcanism, implying that the volcanic release of $CO_2$ was extremely rapid, which is consistent with the sporadic presence of only very thin and discontinuous sedimentary strata between flows (21, 41). However, this does not preclude that a major component of the observed $P_{CO_2}$ increase is contact metamorphic in origin (45), which is hinted at by the small decrease in $^{13}CO_2$ above each flow unit.

The influence of basalt weathering. An intriguing phenomenon recorded by the Newark Basin paleosol sequence is the gradual apparent decrease in $P_{CO_2}$ over time scales of 10$^5$ years after each successive episode of volcanism (Fig. 4). For example, elevated $P_{CO_2}$ values just after the Preakness Basalt in the ~300-ky-long Towaco Formation have nearly returned to pre-eruptive levels by the emplacement of the succeeding Hook Mountain Basalt. We attribute the systematic decrease in $P_{CO_2}$ as the enhanced response of continental silicate weathering consuming each volcanic input of $CO_2$ (46). Given the vast aerial extent of CAMP extrusive activity (27), it is plausible to attribute the rapidity of the decrease in atmospheric $CO_2$ to consumption by hydrolysis.
of the CAMP volcanics themselves, especially in the tropical humid belt where the engines of continental weathering are most effective (47). Geochemical modeling of the period after emplacement of the Deccan LIP and its corresponding CO₂ input show a similar exponential decrease in P CO₂ due to consumption by weathering (Fig. 4) (17). Marine osmium isotope evidence also indicates that an increase in continental weathering followed the CAMP interval (48), lending credibility to a weathering hypothesis. Though the CAMP data correspond well to the initial stages of this modeled decrease, the uppermost portion of the Newark Basin section is truncated, so the full extent of this relation cannot be evaluated here.

**Implications for the end-Triassic extinction.** Neither the Felctville nor Towaco Formations show evidence of P CO₂ changes that can be associated with magmatic events other than those directly related to the observed volcanics. Similarly, the stability of P CO₂ estimates in the Pre-CAMP Passaic Formation leaves the ETE without an obvious P CO₂ precursor. However, the youngest sample in the pre-extrusive section (Exeter Member, Fig. 1) formed in a soil predating the first flow unit by only ~20 ky. This soil occurs two meters below the clay layer containing palynofloral evidence for the ETE in the same exposure, which itself predates the observed onset of volcanism in the Newark by ~19 ky (24). At these sedimentation rates, the uppermost paleosol sample that we studied in the Newark probably pre-dates the ETE by perhaps as little as ~1 ky. Therefore, it is possible that a pulse of CAMP volcanism and an attendant rapid rise in atmospheric P CO₂ with associated climatic implications occurred within the ~20-ky paleosol sampling gap before the age-equivalent of the Orange Mountain Basalt but remain undocumented. Nonetheless, the tight stratigraphic constraint implies that whatever phenomenon caused the ETE must have been very abrupt (occurring within a narrow thousand-year window) or have had minimal effect on atmospheric P CO₂ if it occurred earlier.

**Fig. 4.** (A) Calculated P CO₂ of this study versus time relative to the top of the Orange Mountain Basalt in the Newark Basin (the first CAMP flow unit). The P CO₂ estimates after each successive flow unit in the Newark have been normalized to the initial extrusive event for comparison to a silicate weathering model [colored symbols; error bars are S (z) = 3000 ± 1000 ppm]. (B) Modeled CO₂ consumption due to weathering (17) after emplacement of the Deccan Traps. In the model, a pulse of CO₂ was added to the atmosphere (over 100 ky) accompanying the extrusion of the Deccan LIP. The change in P CO₂ represents the remaining fraction of the total P CO₂ increase in this particular modeling scenario. The abrupt increase of P CO₂ and subsequent postextrusive drawdown found in response to the CAMP volcanism in this study (A) is remarkably similar to the modeling results of Dessert et al. (17), bearing in mind the much longer interval of igneous activity assumed in the model.
CRYPTOCHROME Is a Blue-Light Sensor That Regulates Neuronal Firing Rate

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Light-responsive neural activity in central brain neurons is generally conveyed through opsins-based signaling from external photoreceptors. Large lateral ventral arousal neurons (lLNvs) in Drosophila melanogaster increase action potential firing within seconds in response to light in the absence of all opsin-based photoreceptors. Light-evoked changes in membrane resting potential occur in about 100 milliseconds. The light response is selective for blue wavelengths corresponding to the spectral sensitivity of CRYPTOCHROME (CRY). cry-null lines are light-unresponsive, but restored CRY expression in the lLNv rescues responsiveness. Furthermore, expression of CRY in neurons that are normally unresponsive to light confers low light responsiveness. The CRY-mediated light response requires a flavin redox-based mechanism and depends on potassium channel conductance, but is independent of the classical circadian CRY-TIMELESS interaction.

The Drosophila melanogaster circadian clock circuit is composed of 140 to 150 neurons in the central brain and includes PIGMENT-DISPERSING FACTOR (PDF)—expressing lateral ventral neurons. The large lateral ventral neurons (lLNvs) in Drosophila melanogaster increase action potential firing within seconds in response to light in the absence of all opsin-based photoreceptors. Light-evoked changes in membrane resting potential occur in about 100 milliseconds. The light response is selective for blue wavelengths corresponding to the spectral sensitivity of CRYPTOCHROME (CRY). cry-null lines are light-unresponsive, but restored CRY expression in the lLNv rescues responsiveness. Furthermore, expression of CRY in neurons that are normally unresponsive to light confers low light responsiveness. The CRY-mediated light response requires a flavin redox-based mechanism and depends on potassium channel conductance, but is independent of the classical circadian CRY-TIMELESS interaction.

In addition to the circadian molecular clock, membrane excitability is a key component of normal maintenance of circadian rhythms (14). Electrophysiological characterization of the s- and ILNv has shown that their membrane properties are circadian-regulated outputs as well. Spontaneous firing frequencies are higher during the early day, gradually drop until dusk, and then rise again through the course of the night (1, 15). Additionally, the ILNv spontaneous firing frequency elevates 20 to 200% in response to moderately bright light (4). Given the plurality of light inputs to the ILNv, we investigated the ILNv electrophysiological light response (16) and found that the response is due to CRY acting by a cell-autonomous, redox-based mechanism, independent of CRY-TIM interactions, which requires the conductance of membrane potassium channels. Furthermore, ecotropic expression of CRY optogenetically confers electrophototactic light responsiveness to neurons that ordinarily do not respond to light.

**Results.** Both tonic and burst firing ILNvs recorded in the whole-cell current clamp configuration in an acutely dissected whole-brain preparation from flies expressing the pdf-GAL4 driver and green fluorescent protein (GFP)-tagged nonconducting UAS-dORK, a Drosophila membrane-delimited potassium channel (1, 14), (pdf-GAL4-NCl-GFP) under dark conditions (<0.02 mW/cm²) immediately increased their firing rate and their resting membrane potential in response to moderate-intensity white light (4 mW/cm²) (Fig. 1A, top) or high-intensity blue light (19 mW/cm²) from a mercury light source (450 to 490 nm) (Fig. 1A, bottom), thus rapidly returned to baseline firing rate upon return to darkness. The strength of the firing frequency ILNv light response, expressed here as the firing frequency with the lights on divided by the firing frequency with the lights off (FF on/FF off), varied with light intensity, exhibiting significantly higher firing frequency during lights on compared with lights off at intensities of 2 to 3 mW/cm² or higher (Fig. 1B). FF on/off for 19 mW/cm² was 1.62 ± 0.14 (n = 11) for 4 to 5 mW/cm² was 1.51 ± 0.15 (n = 18), for 2 to 3 mW/cm² was 1.39 ± 0.06 (n = 68), for 1 to 2 mW/cm² was 1.18 ± 0.02 (n = 27), for 0.6 mW/cm² was 1.23 ± 0.06 (n = 16), and for 0.3 mW/cm² was 1.10 ± 0.04 (n = 13). Light responses to intensities of 19 mW/cm², 4 to 5 mW/cm², and 2 to 3 mW/cm² were significantly different from 1 to 2 mW/cm² (P = 0.0001, 0.006, and 0.02, respectively, by analysis of variance (ANOVA)).

The ILNvs anatomically appear to receive input from the compound eye and the HOE eyelet. To determine whether the ILNv light response is due to synaptic inputs from external opsins-based photoreceptors, we recorded ILNv in glasss(60) (g60f) mutant flies, which lack all external photoreceptors because of a null mutation in the eyeless gene (6). The ILNv response to moderate-intensity white light for g60f flies was 1.37 ± 0.09 (n = 14; P = 0.81