Neuronal representation of environmental boundaries in egocentric coordinates

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Movement through space is a fundamental behavior for all animals. Cognitive maps of environments are encoded in the hippocampal formation in an allocentric reference frame, but motor movements that comprise physical navigation are represented within an egocentric reference frame. Allocentric navigational plans must be converted to an egocentric reference frame prior to implementation as overt behavior. Here we describe an egocentric spatial representation of environmental boundaries in the dorsomedial striatum.
he hippocampus, entorhinal cortex, and associated structures store spatial representations in an allocentric or world-centered reference frame that is strongly influenced by environmental boundaries. Computational models suggest that allocentric navigational representations such as boundary responses must arise from and be converted back to an egocentric reference frame to guide overt behavior. The dorsomedial striatum (DMS) shows neural responses related to action decisions, plays a critical role in controlling behavioral output including egocentric navigational strategies, and receives input from regions involved in spatial navigation including medial entorhinal and retrosplenial cortex.

Results

Egocentric boundary coding in DMS. To determine whether egocentric spatial information is present in the DMS, male Long–Evans rats were implanted with up to 16 tetrodes targeting DMS and single units were recorded (n = 939 single units in n = 44 sessions) while rats foraged for randomly scattered food in a familiar open field arena. Stable head direction cells (HDCs, n = 31) were found, similar to previous results in the striatum and other structures, but few cells had allocentric spatial correlates (n = 19 spatially stable cells; Supplementary Fig. 2). However, cells were observed with activity restricted to the environment perimeter only when the rat moved with a particular orientation relative to the walls, suggesting an egocentric coding scheme for boundaries.

To assess the possibility of such an egocentric representation, we created egocentric boundary ratemaps (Fig. 1b, Supplementary Fig. 3) that illustrate the orientation and distance of the boundaries relative to the rat’s movement direction (rather than head direction; Fig. 1g, Supplementary Fig. 3) when a cell spikes. Eighteen percent of recorded cells (171/939 cells) were identified with significant firing when a boundary occupied a specific orientation and distance relative to the animal based on the mean resultant length (MRL) of boundary directional firing exceeding the 99th percentile of a shuffled distribution (Fig. 1f) and responding stably across the two halves of a recording (Supplementary Fig. 3l, m). We termed these egocentric boundary cells (EBCs; EBCs per animal: mean = 42.75, range = 15–70; Fig. 1c, d, Supplementary Fig. 4). A subset of EBCs had firing

![Fig. 1](https://example.com/fig1.jpg)"
rates that decreased in response to a boundary \((n = 49; \text{Fig. 1c})\) that we termed inverse EBCs (iEBCs). EBCs and iEBCs had low mean firing rates \((\text{mean} \pm \text{SEM}: 1.26 \pm 0.09 \text{Hz}, n = 171 \text{cells}; \text{Fig. 1h})\) and virtually all \((97\%)\) fired phasically consistent with them being DMS medium spiny neurons\(^{17}\).

The population of EBCs responds to boundaries at the full spectrum of orientations relative to the animal, although the distribution of preferred orientation is bimodal with peaks sitting 180° opposite each other on either side of the animal \((-68° \text{ and } 112°; \text{Fig. 2, Supplementary Fig. 5})\), while being slightly offset from perpendicular to the animal’s long axis by 22° \((\text{Fig. 2d})\). The offset did not result from a bias in the boundary approach trajectories of the animals \((\text{Supplementary Fig. 5})\), but may stem from a lateraled cortical representation upstream of EBCs and the largely ipsilateral nature of cortico-striatal projections.

The distribution of preferred boundary distance contained three peaks \((6.4, 13.5, \text{and } 25.6 \text{cm})\) indicating the presence of three distinct distribution of preferred boundary distance contained three peaks from a lateralized cortical representation upstream of EBCs and trajectories of the animals \((\text{Supplementary Fig. 5})\), but may stem offset did not result from a bias in the boundary approach. Both preferred orientation and distance lacked clear topography given that EBCs with different orientations and distances appeared on the same tetrode \((\text{Fig. 2a, b, e, f})\).

**EBCs respond stably to local boundaries across environments.** To confirm that EBCs respond to local boundaries rather than distal features of the testing room, we conducted recordings after rotating the open field with four black walls 45° relative to the testing room with numerous static extra-maze cues, putting local boundaries and testing room boundaries maximally out of alignment. Recordings were obtained in the standard and rotated open field orientation \((n = 130 \text{ cells}; n = 4 \text{ sessions})\), including 19 EBCs and 3 HD cells. Following the rotation both the preferred orientation \((\text{Wilcoxon’s signed rank test: } z\text{-score: } -0.63, \text{n.s.}; \text{Fig. 3a, e, Supplementary Fig. 6})\) and preferred distance \((\text{Wilcoxon’s signed rank test: } z\text{-score: } 0.19, \text{n.s.}; z\text{-score: } -1.16, \text{n.s.}; \text{Fig. 3a, e, Supplementary Fig. 6})\) of EBCs remained unchanged. In contrast, HD cells remained anchored to the overall testing room \((\text{Supplementary Fig. 6})\). Given the salience of corners, we considered the possibility that EBCs uniquely code these local environmental attributes and identified a subset of EBCs \((n = 16; 9.4\%)\) with firing rate differences near the corners compared to the middle of the boundaries. This indicates that
EBCs respond to local boundaries of the open field rather than the larger recording room and that egocentric and allocentric reference frames can be computed in parallel\(^7\),\(^8\). To further test EBC responses across different environmental manipulations, we performed recordings in open fields of different sizes, which provides information regarding whether EBCs have a constant preferred distance or instead scale with environment size. Recordings were obtained (\(n = 50\) cells, \(n = 12\) EBCs; \(n = 3\) sessions) in open fields with walls differing in length by 50 cm. Regardless of the size of the open field, EBCs responded to boundaries at the same distance (Wilcoxon’s signed rank test: \(z\)-score: \(-0.71\), n.s.; Fig. 3b, f, Supplementary Fig. 7) and

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**Fig. 3** Egocentric boundary cells (EBCs) respond stably to local environmental boundaries. **a** Egocentric boundary ratemaps with maximum firing rates indicated above each plot, trajectory plots with color-coded movement direction spike locations, and allocentric spatial ratemaps with maximum firing rates indicated above each plot (top to bottom) for an EBC during a baseline and 45° environmental rotation session (left to right). **b** Same plots as in a, but for the standard 1.25 × 1.25 m\(^2\) environment and an expanded 1.75 × 1.75 m\(^2\) environment. **c** Same plots as in a, but for two EBCs (left to right) during recordings with the standard black walls and patterned walls. **d-f** Box plots of preferred distance (top) and change in preferred orientation from baseline (bottom) where the top and bottom of each box represent the first and third quartile, the red line indicates the median and the whiskers indicate the full range of values for (d) the rotation experiment (preferred distance: Base1: 25th: 8.05, 50th: 11.06, 75th: 22.16 cm, Rotate: 25th: 8.42, 50th: 12.88, 75th: 21.54 cm, Base2: 25th: 7.24, 50th: 12.02, 75th: 24.42 cm; preferred orientation: Rotate: 25th percentile: \(-6.15\), 50th percentile: \(-3.21\), 75th percentile: \(5.28^\circ\) change from Base1, Base2: 25th: \(-17.34\), 50th: \(-9.30\), 75th: \(-2.80^\circ\) change from Base1), (e) the expansion experiment (preferred distance: Base: 25th: 6.33, 50th: 16.20, 75th: 28.46 cm; Expand: 25th: 12.51, 50th: 18.68, 75th: 28.58 cm; preferred orientation: Expand: 25th: \(-12.30\), 50th: \(-1.02\), 75th: \(7.02^\circ\) change from Base), (f) the visual appearance experiment (preferred distance: Base1: 25th: 7.96, 50th: 20.74, 75th: 27.44 cm; Pattern1: 25th: 11.21, 50th: 15.65, 75th: 20.67, 75th: 25.69 cm; preferred orientation: Pattern1: 25th: \(-12.10\), 50th: \(-2.04\), 75th: \(9.40^\circ\) change from Base1; Base2: 25th: \(-6.30\), 50th: 0.40, 75th: \(7.80^\circ\) change from Base1)
orientation (Wilcoxon’s signed rank test: z-score: −0.31, n.s.; Fig. 3b, f, Supplementary Fig. 7) from the animal, indicating a lack of scaling with environment size.

The striatum receives input from several visual cortical regions\textsuperscript{14}. Therefore, we asked whether boundary appearance influenced EBC responses. Recordings were performed (n = 73 cells, n = 19 EBCs; n = 4 sessions) in an environment with four black walls and then with three of the walls swapped with walls of different patterns (Fig. 3c, Supplementary Fig. 8). The firing fields of EBCs did not change in either preferred orientation (Wilcoxon’s signed rank test: z-score: −0.63, n.s., z-score: 0.19, n.s.; Fig. 3c, g, Supplementary Fig. 8) or preferred distance (Wilcoxon’s signed rank test: z-score: −0.15, n.s., z-score: −0.63, n.s.; Fig. 3c, g, Supplementary Fig. 8) with the change in visual appearance of the walls. The lack of effect of wall visual appearance on EBCs suggests a higher-order representation of a boundary independent of basic visual features.

The allocentric cognitive map of a given environment maintained in the hippocampal formation is stable over time. We tested whether EBCs maintain a stable representation of a given environment over time by performing two recordings (n = 426 cells, n = 80 EBCs; n = 19 sessions) in the same open field. Both the preferred orientation (Wilcoxon’s signed rank test: z-score: −0.87, n.s.; Supplementary Fig. 9) and preferred distance (Wilcoxon’s signed rank test: z-score: −0.75, n.s.; Supplementary Fig. 9) of EBCs remained stable across sessions. Given the stability of EBC representation for a single environment, we next tested whether EBCs remap across environments as does the allocentric spatial map\textsuperscript{18,19}. Recordings were obtained (n = 38 cells, n = 14 EBCs; n = 2 sessions) as rats explored a familiar and completely novel open field in a novel testing room. EBCs responded with the same preferred orientation (Wilcoxon’s signed rank test: z-score: 1.35, n.s., z-score: −2.04, n.s., z-score: −0.66, n.s.; Fig. 4a, c, Supplementary Fig. 10) and distance

Fig. 4 Egocentric boundary cells (EBCs) do not remap across environments. a Egocentric boundary ratemaps with maximum firing rates indicated above each plot, allocentric spatial ratemaps with maximum firing rates indicated above each plot, and trajectory plots with color-coded movement direction spike locations (top to bottom) for an EBC recorded in a familiar and novel environment (left to right). b Egocentric boundary ratemaps with maximum firing rates indicated above each plot, trajectory plots with color-coded movement direction spike locations, and allocentric spatial ratemaps with maximum firing rates indicated above each plot (top to bottom) for two example EBCs recorded in different familiar environments. c Box plots of preferred distance (top) and change in preferred orientation from baseline (bottom) where the top and bottom of each box represent the first and third quartile, the red line indicates the median and the whiskers indicate the full range of values for the novel environment experiment (preferred distance: Fam1: 25th: 7.68, 50th: 14.32, 75th: 25.73 cm; Nov1: 25th: 7.49, 50th: 12.06, 75th: 23.45 cm; Nov2: 25th: 7.68, 50th: 15.04, 75th: 22.07 cm; Fam2: 25th: 6.67, 50th: 12.62, 75th: 22.07 cm; Nov1: 25th: −10.22, 50th: −4.09, 75th: 1.86° change from Fam1; Nov2: 25th: −0.30, 50th: 6.90, 75th: 12.74° change from Fam1; Fam2: 25th: −3.91, 50th: 0.92, 75th: 12.88° change from Fam1). d Same plots as in c but for the multiple familiar environment experiment (preferred distance: Fam1: 25th: 8.38, 50th: 14.33, 75th: 22.98 cm; Fam2: 25th: 10.75, 50th: 14.80, 75th: 20.39 cm; preferred orientation: Fam2: 25th: −0.23, 50th: 4.43, 75th: 12.85° change from Fam1)
Discussion

The present work identified an egocentric representation of environmental boundaries consistent with theoretical predictions from computational models7,8, which propose that allocentric spatial representations in the hippocampal formation are generated from and converted back to an egocentric spatial representation prior to behavioral output. The striatum receives input from navigation related cortical structures14, including medial entorhinal, retrosplenial, and posterior parietal cortex, but does not directly project to these structures. This suggests that the striatal egocentric representation is not directly involved in the generation of the allocentric spatial representation, while it remains unknown whether the allocentric spatial map is needed to generate the striatal egocentric representation.

Allocentric spatial information could be transformed into an egocentric representation through a process involving allocentric boundary coding cells in medial entorhinal cortex2, and subicular cortices8, postsubicular cells with mixed allocentric-egocentric coding20, and egocentric cells in lateral entorhinal cortex9. Additionally, EBCs in DMS are more strongly coupled to the movement direction of the animal than the animal’s head direction, and movement direction has been proposed to be a potential output of the grid cell network in MEC21. Alternatively, cortical regions such as posterior parietal cortex that contain egocentric sensory and motor representations2–4 could be involved in generating the striatal egocentric representation without allocentric input. The retrosplenial cortex has been proposed as a potential locus for reference frame transformations20, given its efferent and afferent connections with structures that utilize allocentric and egocentric reference frames, while itself utilizing conjunctive allocentric, egocentric, and route-based coding25, and therefore may be an important source of information for generating EBCs in DMS. The data presented here indicates an important egocentric neural representation of boundaries that could interact with allocentric coding of environmental boundaries to guide movement in egocentric coordinates.

Methods

Subjects: Male Long–Evans rats (n = 4) obtained from Charles River Labs (Wilmington, MA, USA) were individually housed in Plexiglass cages in a temperature- and humidity-controlled facility with a 12 h:12 h light:dark cycle. Animals had free access to food and water prior to the initiation of all experiments. All procedures were approved by the Institutional Animal Care and Use Committee at Boston University.

Presurgical procedures: At the start of all experiments, animals were acclimated for at least 2 days to the experimental testing room, to being handled by the researcher, and to eating crushed Froot Loops (General Mills, Battle Creek, MI, USA), which served as the food that animals searched for in the open field. For a minimum of 3 days following that acclimation, animals were exposed to the familiar open fields for up to 20 min/day. The primary familiar open field was 1.25 × 1.25 m2 with black walls 40 cm in height and a dark rubber floor. The secondary familiar open field was 1.25 × 1.00 m2 with grey walls 72 cm in height relative to a black particle board floor that was raised 54 cm off the floor.

Surgical procedures: Aseptic surgery was performed for the implantation of a custom built 12 tetrode hyperdrive targeting the medial striatum. Surgery began with the administration of atropine (0.1 mg/kg) subcutaneously and then anesthesia was induced with a combination of a ketamine cocktail (ketamine: 12.92 mg/kg; acepromazine: 0.1 mg/kg; xylazine: 1.31 mg/kg) administered intraperitoneally and isoflurane administered with a face mask at an initial concentration of 5%. Upon loss of a toe pinch reflex the rat’s head was shaved and the animal was positioned in a stereotaxic frame. A midline incision was made in the rat’s scalp and any connective tissue covering the skull was cleared. Anchor screws were positioned across the skull surrounding the implantation site and the ground screw was positioned over the cerebellum. A craniotomy centered at the hyperdrive implantation site over the medial striatum (AP: + 0.2; M/L: 2.5) was made allowing the medial edge of the hyperdrive to be positioned close to the medial border of the striatum given an approximate 2 mm inner diameter of the cannula housing the tetrodes. Upon completion of the craniotomy, dura was resected and the hyperdrive was lowered using the cannula housing the tetrodes contacted the dorsal surface of the brain. The remaining space in the craniotomy was filled with Kwik-Sil (World Precision Instruments, Sarasota, FL) and the hyperdrive was secured in place by connecting it to the anchor screws with dental cement. Once the hyperdrive was secured in place, the tetrodes were each lowered into the brain. The tetrodes in the first two animals were lowered approximately 4.25 mm, while in the remaining three animals the tetrodes were lowered approximately 3.75 mm to the deep layers of cortex. Post-operative antibiotics (Baytril: 10.0 mg/kg) and analgesics (Ketanest: 5.0 mg/kg) were administered for 5 days and animals were allowed to recover for 7 days with free access to food and water prior to any involvement in experiments.

Electrophysiological recordings: At the start of each day, the rat was placed on an elevated pedestal where it was connected to the electrophysiological acquisition equipment. Neural signals were initially amplified via two headstages attached to a single 64-channel electrode interface board prior to being transmitted to the 64-channel Digital Lynx SX acquisition system (Neuralynx, Bozeman, MT, USA) where the signals were digitized, filtered (0.3–60 kHz), and further amplified (5000–20,000×). Spikes were detected online as a threshold crossing on any of the channels of a tetrode, at which point a window around the threshold crossing time point from each channel of the tetrode was stored for later analysis. Following each experiment, spikes were assigned to individual single units offline using Offline Sorter (Plexon Inc., Dallas, TX, USA). The peak, peak-to-valley, and principal components of the waveforms were utilized for sorting the spikes. The position of the animal was tracked during the recording through the use of a camera positioned over the recording arena. A red and green diode attached to the headstage were tracked in order to obtain both the animal’s position and head direction throughout the recording.

On any given day, an initial 20 min recording was obtained while the rat foraged for small pieces of Froot Loops (General Mills, Battle Creek, MI, USA) scattered on the floor of a familiar open field. The open fields were always open to the testing room, which had a variety of cues. One of several possibilities followed the initial recording depending upon the research question as to whether any day or how EBCs were present during the first recording of the day. In some cases, no more recordings were made that day and tetrodes were generally moved ventrally by approximately 70 µm. On some days, in order to assess the stability of EBCs within a single environment a second 20 min recording in the same familiar open field was conducted. On the remainder of days, one of several different manipulations were performed including:

1. Open field rotation: The standard 1.25 × 1.25 m2 open field was rotated 45° relative to the testing room. Sessions in the rotated open field were preceded and succeeded by standard open field sessions, except for one experiment where a single standard session and a single rotated session were collected.

2. Open field expansion: The standard 1.25 × 1.25 m2 open field could be expanded or contracted to have wall lengths from 1.0 to 1.75 m. Animals were run in three environments dependent upon the research question, namely: a) the standard 1.25 × 1.25 m2 environment, b) the 1.75 × 1.75 m2 open field, c) the 1.0 × 1.5 m2 open field. Recordings performed in the 1.75 × 1.75 m2 open field lasted longer in order to obtain adequate spatial coverage of the environment. Expansion experiments minimally included recordings in square environments with walls differing by 50 cm, but also included a recording in the standard 1.25 × 1.25 m2 when the 1.0 and 1.5 m long walls were used.

3. Visual appearance: The standard 1.25 × 1.25 m2 open field had four black walls that could be swapped for walls with different patterns. Three of the four walls were changed from the standard black walls to one of three different walls including an all white wall, a black wall with thin diagonal white stripes and a wall with black and white vertical stripes of equal widths. A 4 × 4 array of single sessions with two sessions in the environment with the patterned walls preceded and succeeded by a session with all black walls. One experiment only included a single session with the patterned walls flanked by sessions with all black walls.
4. Multiple familiar environments: Animals were run in the standard 1.25 × 1.25 m² open field and then the alternative 1.00 × 1.25 m² familiar open field described above in presurgical procedures. All animals had a minimum of 8 days of exposure to each open field prior to any recordings. One recording in each familiar environment was collected.

5. Novel open field: Animals were first run in the standard 1.25 × 1.25 m² open field and then brought into an adjacent testing room they had never been in previously. In this novel testing room, rats were recorded while they foraged in a novel square open field that had a smooth white floor and 1.25 m long black walls that were 30.5 cm tall. A sequence of four recordings was collected including two sessions in the novel environment and two sessions in the familiar environment with one preceding and one succeeding the novel environment sessions.

Histology: Animals were deeply anesthetized with isoflurane and small lesions were made at the end of tetrodes that had preliminarily been identified as having EBCs. The lesions were made by passing a small 20 µA current through each channel of the tetrode for 10 s. After the lesions were made, the animals were transcardially perfused with 0.9% saline followed by 10% formalin solution. The brain was then removed from the skull and post-fixed in 10% formalin until it was sliced. To generate the final ratemaps, the 2D firing rate histogram was color coded from 0 (blue) to the maximum of the firing rate distribution (red) with that maximum firing rate value specified above the top-left corner of each allocentric spatial ratemap. Spatial bins with insufficient occupancy to calculate a firing rate appear as white in the ratemaps.

Allocentric spatial ratemap generation: The open field arena was divided into equally sized spatial bins (3 × 3 cm²) and the firing rate within each spatial bin was calculated as the number of spikes occurring in a given bin divided by the amount of time the animal spent in the bin. The resulting occupancy normalized two-dimensional (2D) firing rate histograms were smoothed with a 2D 3 cm Gaussian Kernel (Supplementary Fig. 3c). The data were considered in an allocentric reference frame where the boundary position was considered relative to a static rat position (Supplementary Fig. 1). In order to ensure that cells maintained a consistent representation throughout the initial recording session, the session was divided into halves and cells were classified as EBCs if all of the following criteria were met: (1) mean firing rate was >0.1 Hz, (2) MRL for both the 1st and 2nd half was greater than the 99th percentile of the shuffled distribution, (3) the change in MRA between the 1st and 2nd half was <45°, and (4) the change in preferred boundary distance between the 1st and 2nd half was <75% of the preferred distance for the whole session. The cells meeting these criteria were then clustered using the k-means clustering algorithm using firing rate, boundary direction MRA, Preferred boundary distance, PropDist × 2 (see below), allocentric ratemap coherence, allocentric ratemap dispersion, and field size values ranging from 25 to 85% of the maximum firing rate (10% steps) as features.

HDC classification: The MRL Rm was calculated for each cell as

$$R_m = \frac{\cos(\theta) \sum_{n=1}^{N_m} F_n \cos(\theta_n) + \sin(\theta) \sum_{n=1}^{N_m} F_n \sin(\theta_n)}{\sum_{n=1}^{N_m} F_n},$$

where \(\theta\) was the head direction of firing and \(F\) and \(\theta\) were the firing rate and head direction for bin \(i\). HDCs were identified as those cells with \(R_m < 0.3\). Spatially stable allocentric cell classification: Cells with stable allocentric firing were identified as those cells with allocentric ratemaps for the two halves of a recording with a correlation >0.5 that were not already identified as either EBCs or HDCs.

EBC firing rate vs. tonic firing: Previous reports identified striatal cells with phasic or tonic spiking properties. Cell classification as phasic or tonic firing was based on post-spike suppression (PSS) and the proportion of interspike intervals (ISIs) shorter than 2 s (PropISI < 2 s). PSS quantifies the amount of time that it takes a cell to return to its mean firing rate following a spike. Using a 1 s window with 1 ms bins, the autocorrelation of each cell’s spike train was computed and smoothed with a 25 ms Hamming window. The duration of time following a spike for the firing rate to reach the mean was taken as the PSS. The proportion of time that a cell spends in long interval ISIs provides a measure of the regularity with which a cell spikes and was measured as the summation of all ISIs >2 s divided by the total session length. Cells with PropISI < 0.4 were classified as phasically firing neurons, while cells with PropISI < 0.4 and PSS < 100 ms were classified as high firing neurons. As noted in the main text, almost all EBCs and iEBCs (97%) fired phasically.

Mixed Gaussian models: Distributions of preferred orientation or preferred direction were modeled as mixtures of Gaussian distributions using varying orders from 1 to 10. The optimal model was identified as the model that minimized the Akaike information criterion. The local maxima in the probability distribution.
function of the optimal model greater than the mean of the probability density function were identified and reported as the peaks of the distribution. This process was conducted on the data obtained from each individual animal (Supplementary Fig. 5f–i) and the distributions of peaks obtained from the individual animals were fit with Gaussian mixture models again allowing for a range of orders from 1 to 20 and identifying the optimal model as that which minimized the Akaike information criterion. The outcome of this approach is in line with fitting the distributions of preferred orientation and preferred distance for all EBCs with Gaussian mixture models and identifying the peaks of those models (compare Fig. 2d, h to Supplementary Fig. 5d, f).

**Statistics.** Non-parametric statistics were used for all post hoc comparisons as the normality of the distributions was not assumed. Two-sided Wilcoxon’s signed rank tests were used with a p value threshold of 0.01 for all comparisons. The values reported throughout the text are the 25th, 50th, and 75th percentile of the relevant distribution.

**Reporting summary.** Further information on research design is available in the Nature Research Reporting Summary linked to this article.

**Data availability**
The data used in this study are available from the corresponding author upon reasonable request.

**Code availability**
The custom written code used to analyze the data in this study is available from the corresponding author upon reasonable request.

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**Author contributions**
J.R.H. and M.E.H. designed the study. J.R.H. conducted all aspects of the experiments. J.R.H. and G.W.C. analyzed the data. J.R.H. and M.E.H. wrote the paper and G.W.C. provided feedback on the paper.

**Additional information**

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