


“Walking selectivity” in the occipital place area in 8-year-olds, not 5-year-olds

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A recent neuroimaging study in adults found that the occipital place area (OPA)—a cortical region involved in “visually guided navigation” (i.e. moving about the immediately visible environment, avoiding boundaries, and obstacles)—represents visual information about walking, not crawling, suggesting that OPA is late developing, emerging only when children are walking, not beforehand. But when precisely does this “walking selectivity” in OPA emerge—when children first begin to walk in early childhood, or perhaps counterintuitively, much later in childhood, around 8 years of age, when children are adult-like walking? To directly test these two hypotheses, using functional magnetic resonance imaging (fMRI) in two groups of children, 5- and 8-year-olds, we measured the responses in OPA to first-person perspective videos through scenes from a “walking” perspective, as well as three control perspectives (“crawling,” “flying,” and “scrambled”). We found that the OPA in 8-year-olds—like adults—exhibited walking selectivity (i.e. responding significantly more to the walking videos than to any of the others, and no significant differences across the crawling, flying, and scrambled videos), while the OPA in 5-year-olds exhibited no walking selectivity. These findings reveal that OPA undergoes protracted development, with walking selectivity only emerging around 8 years of age.

Key words: Development; locomotion; visually guided navigation; fMRI; occipital place area.

Introduction

As humans, we are exquisite at finding our way through a place—a living room, an office, or a restaurant, for example—without running into the walls or banging into the furniture. This process, often referred to as “visually guided navigation,” forms the bedrock for many of our essential everyday behaviors. Given this ecological importance, it is perhaps not surprising that we have a cortical region—the occipital place area (OPA) (Dilks et al. 2013)—devoted to visually guided navigation (Dilks et al. 2011, 2013; Kamps et al. 2016; Bonner and Epstein 2017; Persichetti and Dilks 2018; Park and Park 2020; Dilks et al. 2022). However, despite our growing understanding of the visually guided navigation system (including OPA) in adults, a fundamental question remains: How does this system develop?

A recent functional magnetic resonance imaging (fMRI) study in adults (Jones et al. 2023) sheds some light on this question, revealing that OPA represents visual information from only one perspective by which humans move about their local visual environments (i.e. walking) and not from a perspective by which we had done so much earlier in life (i.e. crawling). Based on this finding, one intuitive hypothesis is that OPA develops when children first begin to walk, around the first year of life. By contrast, however, several behavioral studies found that there is a significant change in walking skills in children until around 8 years of age, due to improving gait speed and obstacle avoidance (Pryde et al. 1997; Berard and Vallis 2006; Michel et al. 2010), the presence of adult-like ankle kinetics (Chester et al. 2006), and more efficient foot placements (Berard and Vallis 2006; Choi et al. 2016; Corporaal et al. 2018). Thus, these studies lead to another, perhaps counterintuitive, hypothesis that OPA develops much

later in childhood, around 8 years of age, when children become “adult” walkers.

Here, we directly test these two hypotheses by examining when “walking selectivity” in OPA first emerges in development. Specifically, using fMRI, we measured the responses in OPA in children 5 years and 8 years of age while they watched videos depicting the first-person visual experience of moving through scenes from a “walking” perspective, and three control perspectives (i.e. “crawling,” “flying,” and “scrambled”; Fig. 1). If walking selectivity (i.e. a significantly greater response to the walking videos compared to all other perspectives and no significant difference across crawling, flying, and scrambled) is present when children first begin to walk, then OPA will exhibit walking selectivity in both 5-year-olds and 8-year-olds. By contrast, if walking selectivity emerges much later in childhood, not until around 8 years of age when children are adult-like walking, then OPA will exhibit walking selectivity in 8-year-olds only, not 5-year-olds. Importantly, fMRI data quality was matched between the two age groups (Fig. 2A–C), ensuring that data quality could not account for any observed developmental differences.

Materials and methods

Participants

Eighteen children at the age of 8 years (mean age = 101.8 months, range = 96–108 months, 7 females) and 22 children at the age of 5 years (mean age = 65.4 months, range = 55–72 months, 13 females) participated in experiment 1 (with the adult perspective videos). Four 5-year-olds were excluded either because they did not complete the minimum two runs for the main experiment ($n=2$) or because of their excessive motion and/or lack of

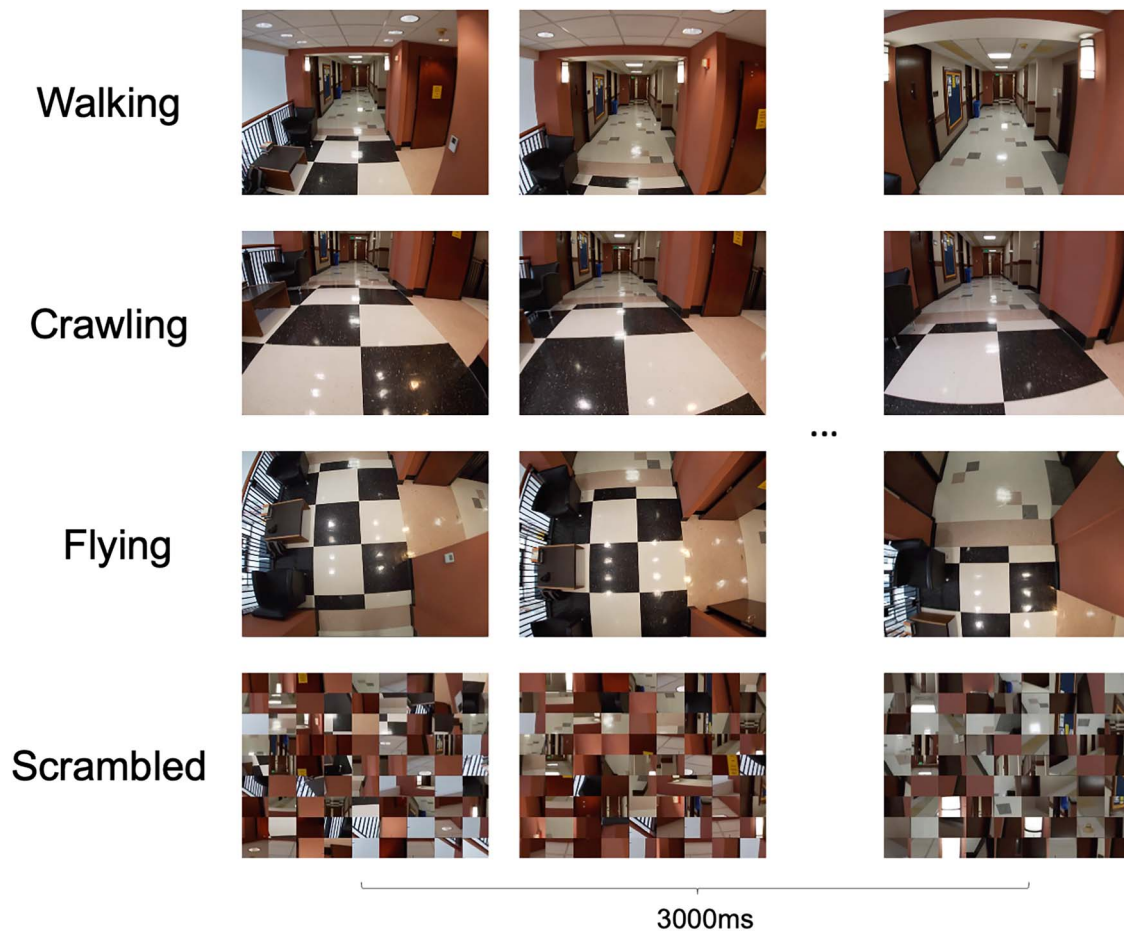


Fig. 1. Example frames from the “walking,” “crawling,” “flying,” and “scrambled” videos.

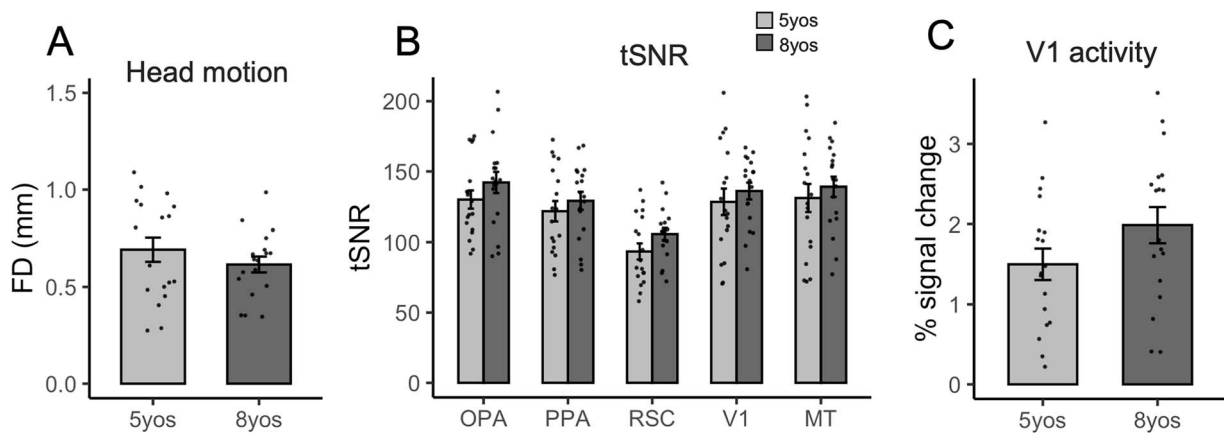


Fig. 2. Data quality did not differ between the 5-year-olds and the 8-year-olds. No significant differences were found between the two age groups for any of the following measures: A) participant head motion (average absolute frame-to-frame displacement of all usable runs; $t(34) = -1.02$, $P = 0.32$, $d = 0.34$); B) temporal signal-to-noise ratio (tSNR) in any region of interest (all t 's < 1.72 , all P 's > 0.09 , all d 's < 0.57); or C) V1 activation (i.e. the average response in V1 across all conditions compared to fixation; $t(34) = 1.63$, $P = 0.11$, $d = 0.54$).

attention during runs ($n = 2$; see below for the exclusion criteria). Thus, the final sample of 18 4- to 5-year-olds were included in experiment 1. In experiment 2 (with the 5-year-old perspective videos), another group of 10 children aged 5 years (mean age = 63.3 months, range = 59–67 months, 4 females) were recruited, and none were excluded.

All participants were recruited through the Emory Child Study Center. Consent was given for all children by their parent or guardian, and verbal assent was additionally collected for the

8-year-olds. All participants had normal or corrected to normal vision, and no history of neurological or psychiatric conditions. All procedures were approved by the Emory University Institutional Review Board.

Design and stimuli

We used a region of interest (ROI) approach in which we used one set of runs to localize scene-selective ROIs and a second

set to investigate the responses of these same voxels. This ROI approach was facilitated by a group-constrained, subject-specific (GSS) method, as detailed in the Data Analysis section.

For all runs, a blocked design was used in which participants watched videos from four different “scene” conditions (i.e. “walking,” “crawling,” “flying,” and “scrambled”) and one “object” condition. The scene stimuli consisted of 12 3-second video clips depicting first-person perspective motion and subtended approximately 15.7×20.7 degrees of visual angle. The object stimuli consisted of 12 3-second video clips of everyday objects moving, as previously described (Pitcher et al. 2011) and also subtended approximately 15.7×20.7 degrees of visual angle. Each run was 312 seconds long and contained 2 blocks of each condition. The order of the first set of blocks was pseudorandomized across participants (e.g. walking, flying, crawling, object, and scrambled), and the order of the second set of blocks was the palindrome of the first (e.g. scrambled, object, crawling, flying, and walking). Each block started with a picture that describes the condition (e.g. a crawling baby for the crawling condition), which was presented for 2 seconds, followed by six 3-second videos with an ISI of 0.5 seconds. Participants were asked to actively imagine themselves walking, crawling, or flying in different places (for the walking, crawling, and flying conditions), being a monster with many eyes (for the scrambled condition), and playing with the toys (for the object condition) while watching the videos. There were also three 12-second fixation blocks at the beginning, in the middle, and at the end of each run.

The scene videos used in this experiment were the same as those used in Jones et al. (2023). To reiterate, the videos were filmed using a GoPro camera. For the walking videos, the videos were taken while an experimenter walked through 12 different places with the camera attached to his forehead (e.g. a backyard, a hallway, and a park). For the crawling videos, the videos were taken while the same experimenter, with the camera attached to his forehead, crawled through the same 12 places. Note that while crawling, the experimenter kept his head up and his eyes forward, as babies do (see Jones et al. 2023 for details). For the flying videos, the GoPro camera was mounted on a rod and held approximately 10 feet in the air, facing down at the ground, while the experimenter walked through the same 12 places—to mimic a bird’s-eye view, which is a perspective from which humans do not navigate. Finally, for the scrambled videos, the walking videos were divided into a 9×9 grid, and the cells were randomly shuffled within the grid to scramble the video. The scrambled order of the 9×9 cells remained the same throughout each video clip, and the temporal order was kept intact.

In experiment 2, all aspects of the study were identical to experiment 1, except for the scene videos, which were now filmed using a group of four children at the age of 5 years (mean age = 65 months, range = 63–67 months, 2 females, mean height = 43.01 inches, range of height = 40–45.3 inches). These children wore a GoPro camera while they were either walking or crawling around 12 different places. Each child filmed the videos in three different places, both while walking and crawling as they typically would. For flying videos, an adult experimenter filmed the “flying” perspective with a rod in the same places where children walked and crawled. Finally, scrambled videos were created using the walking videos, as described in experiment 1.

During each scanning session, we first took a high-resolution anatomical scan while the children watched a movie or show of their choice. Then, we collected fMRI data while participants viewed the videos from “walking,” “crawling,” “flying,”

“scrambled,” and “object” conditions (as described above) for 4 runs. After the first two runs, we took a 6-minute resting-state scan while participants again watched a movie or show of their choice. Data from this resting-state scan is not included in the current study.

Functional magnetic resonance imaging (fMRI) scanning

All scanning was performed on a 3 T Siemens Trio scanner in the Facility for Education and Research in Neuroscience at Emory University. The functional images were collected using a 32-channel head matrix coil and a gradient-echo single-shot echoplanar imaging sequence (28 slices, TR = 2 s, TE = 30 msec, voxel size = $1.5 \times 1.5 \times 2.5$ mm, and a 0.5 interslice gap). For all scans, slices were oriented approximately to AC-PC, covering all the occipital and temporal lobes, as well as the lower portion of the parietal lobe. Additionally, whole-brain, high-resolution anatomical images were acquired for each participant for registration and anatomical localization.

Behavioral experiment

After the fMRI experiment in experiment 1, participants completed a behavioral experiment where they were presented with walking or crawling videos and asked to determine whether the video depicted walking or crawling (Perspective Judgment Task). Similar to the fMRI experiment, each video was 3-seconds long, and participants responded verbally (i.e. “walking” or “crawling”) after watching each video. Participants also performed a control task, where they were asked to determine whether the video depicted an indoor or outdoor setting. The order of the tasks (the perspective judgment task and the control task) was counter-balanced across participants. Note that two 5-year-olds and four 8-year-olds did not complete the behavioral experiment, leaving a total sample of 16 5-year-olds (mean age = 64.9 months; 7 females) and 14 8-year-olds (mean age = 102.7 months, 5 females) for this analysis.

Data analysis

Preprocessing was performed using AFNI (Cox 1996) (version 20.3.02). MRI data from the experiment runs were registered to a T1w reference using `align_epi_anat.py` (AFNI) and corrected for head-motion using `3dvolreg` (AFNI). Before motion correction, volumes with movement > 2 mm were corrected via interpolation between the nearest nonaffected volumes to reduce abrupt signal changes caused by head motion (`3dDespike`, AFNI). Spatial smoothing was applied with a Gaussian kernel with a 6 mm full width at half maximum (FWHM) using `3dmerge` in AFNI. Temporal smoothing was performed to remove frequencies above 0.2 Hz. Head-motion parameters with respect to the BOLD reference were estimated before any spatial or temporal smoothing.

To ensure the data quality of our sample, we excluded runs where the average absolute frame-to-frame displacement was greater than 1.5 mm (i.e. the approximate size of one voxel) and where activation could not be detected in V1 ($Z < 2.3$). Further, we only included children who had at least two runs that met these criteria, since at least two runs are required for the GSS method, which uses independent sets of runs to localize and test responses in each ROI (see Data Analysis). These criteria resulted in the exclusion of four 5-year-olds (all 8-year-olds met these criteria) in experiment 1. As a result of these procedures, the final groups of 5- and 8-year-olds from experiment 1 were matched on

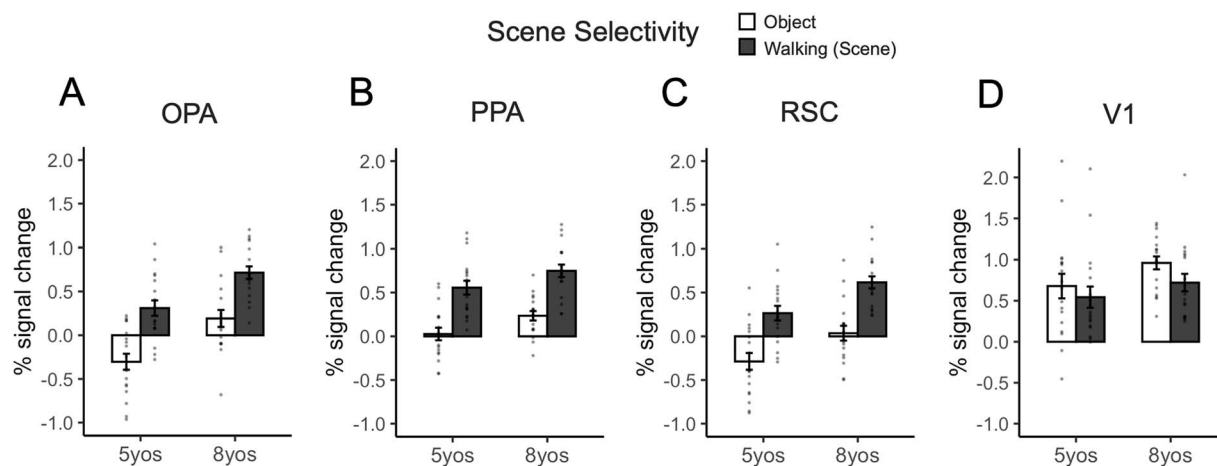


Fig. 3. Average percent signal change to the walking videos (or “scenes”; dark gray) and the object videos (white) relative to fixation in A) OPA, B) PPA, C) RSC, and D) V1, labeled accordingly, in 5-year-olds and 8-year-olds. Error bars depict the standard error of the mean.

head motion ($t(34) = -1.0202$, $P = 0.315$, $d = -0.34$; Fig. 2A), temporal signal-to-noise ratio (tSNR) in all ROIs (all t 's < 1.72 , all p 's > 0.09 , all d 's < 0.57 ; Fig. 2B), and V1 activation (i.e. the average response in V1 across all conditions, $t(34) = 1.63$, $P = 0.11$, $d = 0.54$) (Fig. 2C). The number of usable runs from each subject across the group was also comparable in experiment 1 (mean number of usable runs in 5-year-olds = 3.16, mean usable runs in 8-year-olds = 3.27, $t(34) = 0.39$, $P = 0.695$, $d = 0.07$): for the final sample of 5-year-olds, 8 participants had 4 usable runs, 5 participants had 3 usable runs, and 5 participants had 2 runs; for the final sample of 8-year-olds, 9 participants had 4 runs, 5 participants had 3 runs, and 4 participants had 2 runs. In experiment 2, 6 participants had 4 usable runs, 1 participant had 3 usable runs, and 3 participants had 2 usable runs (average number of usable runs = 3.3).

ROIs were defined using the Group-Constrained Subject-Specific (GSS) method (Julian et al. 2012). The GSS analysis was conducted using the following procedure. First, for each participant, we identified a search space for each ROI using previously published probabilistic atlases that predict the location in which each ROI is likely to fall given the typical distribution found in a large sample of adults. Search spaces for scene-selective regions were derived from Julian et al. (2012), while search spaces for MT and V1 were derived from Wang et al. (2015). Second, for each search space in each participant, voxels were ranked using the data from one run, based on parameter estimates for the contrasts of walking videos (scenes) > object videos (for the scene-selective regions), or all conditions > fixation (for MT and V1). Based on these rankings, the top 10% of the voxels were then selected as the subject-specific ROI. By selecting the top 10% of voxels with peak scene selectivity, we avoided possible overlap of OPA and nearby retinotopic regions (i.e. LO1, LO2, V3a, V3b, and V7; see Silson et al. 2016, Lescroart and Gallant 2019). Also, note that when selecting the voxels, we did not enforce spatial continuity. Nevertheless, when the selected voxels were visualized, the majority of these selective voxels formed a contiguous cluster. Third, responses to each condition in each ROI and participant were measured using the remaining, independent runs. Fourth, this same define-then-test procedure was repeated across every possible permutation of the runs (leave-one-run-out). Finally, we averaged the results of each possible permutation together, resulting in the final estimate of responses to the four conditions for each ROI in each participant. The datasets generated during this study are available at <https://osf.io/g65hj/>.

In addition to the ROI analysis described above, we also performed a group-level whole-brain univariate analysis to explore how visual information about walking is represented in 5-year-olds' brains. For this analysis, we registered the data from the subject space to the MNI space and performed a conjunction univariate analysis where we looked for voxels that showed significantly greater response to walking videos than any other condition (i.e. walking > crawling, “and” walking > flying, “and” walking > scrambled). We combined the data from the experiment with the adult perspective videos ($n = 18$) and the data from the experiment with the 5-year-old perspective video ($n = 10$) for this analysis as the ROI analysis showed a similar pattern of responses across the two experiments. The resulting statistical maps were thresholded at $P < 0.05$, and the cluster-based multiple comparison correction was performed at a voxel size > 295 .

Results

Occipital place area (OPA) is scene-selective by 5 years of age

Before investigating walking selectivity in OPA, we first asked whether “scene selectivity” could be detected in OPA in 5-year-olds, as previously shown (Kamps et al. 2020), by comparing responses in OPA to the walking videos (“scenes”) to object videos (another condition of stimuli included, see Materials and Methods)—following the standard contrast (i.e. scenes minus objects) used to define OPA in adults (Dilks et al. 2011, 2013). A 2 (group: 5-year-olds, 8-year-olds) \times 2 (condition: walking, object) mixed model ANOVA revealed a significant main effect of condition ($F(1,34) = 35.18$, $P < 0.001$, $\eta_p^2 = 0.51$), with stronger responses to the walking than object videos, but no significant group by condition interaction ($F(1,34) = 0.22$, $P = 0.64$, $\eta_p^2 = 0.01$; Fig. 3A). These findings show that scene selectivity is present in OPA by 5 years of age and is already of similar magnitude to that observed by 8 years of age (Fig. 3A).

For completeness, we also investigated scene selectivity in two additional cortical regions involved in other aspects of scene processing (not visually guided navigation), including the parahippocampal place area (PPA) and the retrosplenial cortex (RSC) (Dilks et al. 2022). For both PPA and RSC, a 2 (group: 5-year-olds, 8-year-olds) \times 2 (condition: walking, object) mixed effect model ANOVA revealed a significant main effect of condition (for PPA: $F(1,34) = 133.22$, $P < 0.001$, $\eta_p^2 = 0.80$; for RSC: $F(1,34) = 142.54$,

$P < 0.001$, $\eta_p^2 = 0.81$), but no significant group by condition interaction (for PPA: $F(1,34) = 0.03$, $P = 0.86$, $\eta_p^2 = 0.001$; Fig. 3B; for RSC: $F(1,34) = 0.09$, $P = 0.76$, $\eta_p^2 = 0.003$; Fig. 3C). These findings show that scene selectivity is present in PPA and RSC, like OPA, by 5 years of age, with no changes in scene selectivity across ages 5 to 8 years—again replicating a previous finding (Kamps et al. 2020).

To confirm that the findings above were driven by scene selectivity, rather than stimulus complexity (i.e. low-level visual information differences), we also investigated responses in V1. Unlike the three scene-selective regions, a 2 (group: 5-year-olds, 8-year-olds) \times 2 (condition: walking, object) mixed effect ANOVA did not reveal a significant main effect of condition ($F(1,34) = 2.68$, $P = 0.11$, $\eta_p^2 = 0.073$) or a significant group by condition interaction ($F(1,34) = 0.323$, $P = 0.573$, $\eta_p^2 = 0.009$; Fig. 3D). Furthermore, comparing V1 to each scene-selective region directly, a 2 (ROI: V1, each scene-selective region) \times 2 (condition: walking, object) repeated-measures ANOVA revealed a significant ROI by condition interaction (all $F > 35.8$, all $P < 0.001$, all $\eta_p^2 > 0.51$). Thus, responses in OPA, PPA, and RSC indeed reflect scene selectivity, not stimulus complexity.

Occipital place area (OPA) represents visual information about walking in 8-year-olds, but not in 5-year-olds

Having established that OPA is scene-selective in children 5 years of age, we next turned to our main question: When does walking selectivity in OPA emerge in development? Interestingly, we found that walking selectivity in OPA is observed in 8-year-olds only, not in 5-year-olds (Fig. 4A). “Walking selectivity” is defined as: (i) a significantly greater response to the walking videos than to any of the other videos and (ii) no significant difference across the crawling, flying, and scrambled videos, as previously described (Jones et al. 2023). Specifically, in 8-year-olds, a 4-level (walking, crawling, flying, and scrambled) repeated-measures ANOVA revealed a significant main effect ($F(3,51) = 9.10$, $P < 0.001$, $\eta_p^2 = 0.35$), with significantly stronger responses to the walking videos than to any of the others (main effect contrasts; all P 's > 0.002). No significant differences were found between the crawling versus flying videos ($P = 0.548$), crawling versus scrambled videos ($P = 0.262$), or flying versus scrambled videos ($P = 0.08$). These findings, therefore, reveal that OPA in 8-year-olds, like adults, is selective for walking. In 5-year-olds, however, although a 4-level (walking, crawling, flying, and scrambled) repeated-measures ANOVA again revealed a significant main effect ($F(3,51) = 9.09$, $P < 0.001$, $\eta_p^2 = 0.35$), the response in OPA to the walking videos was not significantly greater than to either the crawling (main effect contrast; $P = 0.95$) or flying videos ($P = 0.843$). By contrast, significant differences were found between each of the walking, crawling, and flying videos compared to the scrambled ones (all P 's < 0.001). Taken together, these findings reveal that the OPA in 5-year-olds, unlike 8-year-olds (and adults), does not exhibit walking selectivity. Critically, directly comparing the 5-year-olds and the 8-year-olds then, a 2 (group: 5-year-olds, 8-year-olds) \times 4 (condition: walking, crawling, flying, scrambled) mixed-model ANOVA revealed a significant group by condition interaction ($F(3,102) = 3.476$, $P = 0.019$, $\eta_p^2 = 0.093$), revealing a qualitatively different pattern between the two groups, with walking selectivity in OPA present in children 8 years of age, not 5 years of age.

Note, however, that the walking selectivity in the OPA of 8-year-olds and the lack of walking selectivity in the OPA of 5-year-olds are based on null effects. More specifically, in 8-year-olds,

the walking selectivity in OPA is driven by similar responses to the crawling, flying, and scrambled videos. Similarly, in 5-year-olds, the lack of walking selectivity is driven by similar responses to the walking, crawling, and flying videos. Thus, it is possible that we simply failed to find an effect in either of these groups. To test this possibility, we conducted two additional analyses in both groups in two ways. First, we conducted a nonparametric ANOVA, by generating a null F -statistic distribution and comparing the true F -statistics to this null distribution. To do so, we first randomly shuffled the labels of the conditions within each participant and conducted a repeated-measure ANOVA with three levels (i.e. crawling, flying, and scrambled in 8-year-olds; walking, crawling, and flying in 5-year-olds) with the shuffled labels. We then repeated this procedure 10,000 times, which resulted in a null distribution of 10,000 F -statistics. These analyses revealed no significant main effect of condition in 8-year-olds ($P = 0.153$) and no significant main effect of condition in 5-year-olds ($P = 0.941$). Second, we also conducted Bayesian repeated-measures ANOVAs in both groups, which resulted in a Bayes factor of 0.58 in 8-year-olds [suggesting that the null hypothesis is 1.72 (100/58) times as likely as the alternative hypothesis] and a Bayes factor of 0.15 in 5-year-olds [suggesting that the null hypothesis is 6.66 (100/15) times as likely as the alternative hypothesis]. Taken together, these additional analyses confirm that: (i) the OPA in 8-year-olds represents visual information about walking only, as the response in the OPA to the crawling videos is not significantly different from the flying and scrambled ones and (ii) OPA in 5-year-olds does not represent visual information about walking, as the response in the OPA to the walking videos is not significantly different from the crawling and flying ones.

But does this developmental difference in OPA reflect sensitivity to visual information about walking specifically or instead a developmental difference in motion sensitivity more generally—as it could be the case that the walking videos simply contain more motion information than the other videos. To address this question, we compared the responses in OPA with those in the middle temporal area (MT), a general motion-sensitive region. For MT, a 2 (group: 5-year-olds, 8-year-olds) \times 4 (condition: walking, crawling, flying, scrambled) mixed-model ANOVA did not reveal a significant group by condition interaction ($F(3,102) = 0.80$, $P = 0.50$, $\eta_p^2 = 0.006$), but rather revealed a main effect of condition ($F(3,102) = 5.02$, $P = 0.003$, $\eta_p^2 = 0.023$), with a significantly greater response to the scrambled videos than to the walking videos ($P < 0.001$), the crawling videos ($P = 0.003$), and the flying videos ($P = 0.033$) (Fig. 4B). These findings suggest that MT, unlike OPA, does not respond more to the walking videos than to any of the others, and does not differ between the 5-year-olds and 8-year-olds. Testing this claim directly, a 2 (group: 5-year-olds, 8-year-olds) \times 2 (ROI: OPA, MT) \times 4 (condition: walking, crawling, flying, scrambled) mixed-model ANOVA revealed a significant group by ROI by condition interaction ($F(3,102) = 2.39$, $P = 0.03$, $\eta_p^2 = 0.07$), ruling out the possibility that the walking videos simply contained more motion information and thus can explain the developmental difference in walking selectivity in OPA.

Finally, we asked whether the developmental difference in walking selectivity in OPA is indeed specific to OPA. To address this question, we compared OPA to PPA and OPA to RSC. A 2 (group: 5-year-olds, 8-year-olds) \times 2 (ROI: OPA, PPA, or RSC) \times 4 (condition: walking, crawling, flying, scrambled) mixed-model ANOVA revealed a significant group by ROI by condition interaction for both OPA and PPA ($F(3,102) = 4.581$, $P = 0.005$, $\eta_p^2 = 0.119$) and OPA and RSC ($F(3,102) = 3.20$, $P = 0.03$, $\eta_p^2 = 0.09$; Fig. 4C and D), demonstrating that the developmental difference in walking selectivity

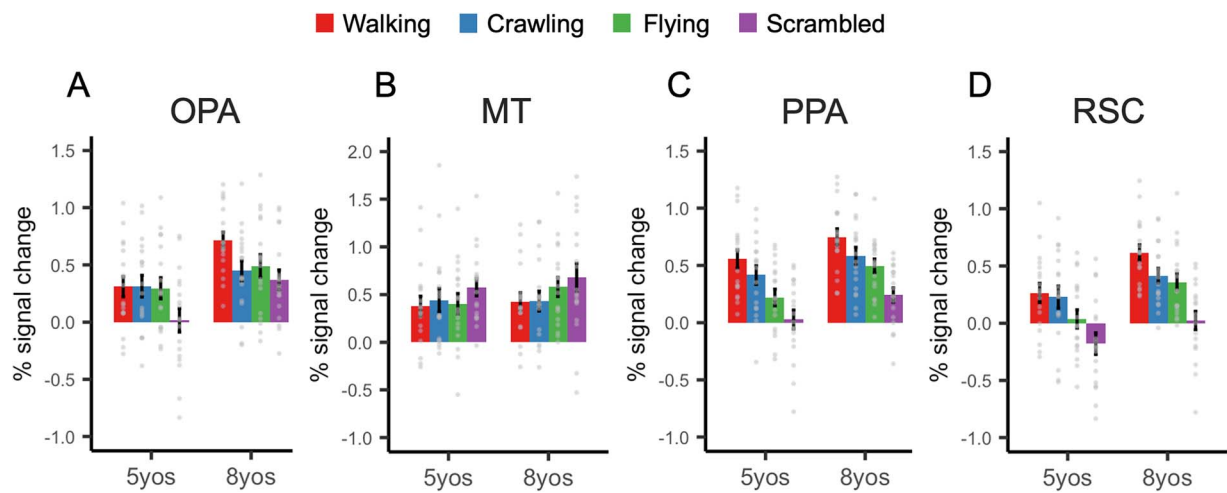


Fig. 4. Responses to the walking, crawling, flying, and scrambled videos from adult perspective in A) OPA, B) MT, C) PPA, and D) RSC, relative to fixation. In OPA, 5-year-olds and 8-year-olds show different patterns of responses: 8-year-olds show selectivity to walking (i.e. greater than all other conditions), while 5-year-olds show similar responses to walking, crawling, and flying videos. In contrast, in PPA and RSC, both the 5- and 8-year-olds show similar patterns of responses, indicating that the data quality is comparable between 5 years and 8 years. These findings reveal that OPA does not represent information about walking in 5-year-olds but only does so in 8-year-olds. Error bars depict the standard error of the mean, and individual data points are plotted as gray dots.

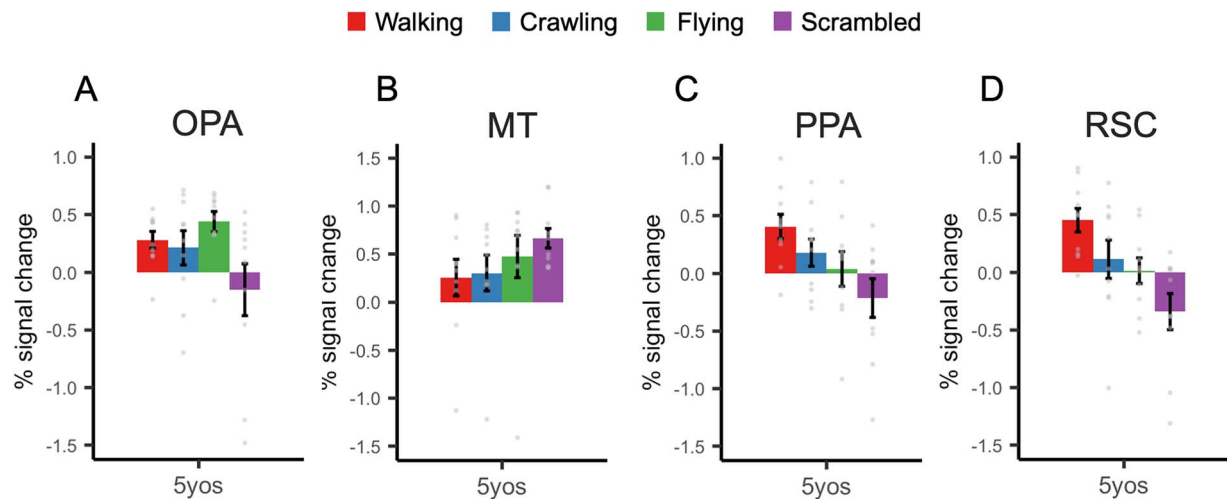


Fig. 5. Responses to the walking, crawling, flying, and scrambled videos from a 5-year-old perspective in A) OPA, B) MT, C) PPA, and D) RSC in a new group of 5-year-olds ($n = 10$), relative to fixation. Error bars depict the standard error of the mean, and individual data points are plotted as gray dots.

in OPA is specific to OPA. Note that neither PPA nor RSC, unlike OPA, exhibit walking selectivity at all (i.e. they each respond significantly more to the walking videos than to the crawling videos, more to the crawling videos than to the flying videos, and more to the flying videos than to the scrambled videos, all P 's < 0.016), consistent with their hypothesized roles in other aspects of scene processing (Dilks et al. 2022). These results also rule out the possibility that 5-year-olds were simply paying less attention to the walking videos than the 8-year-olds, since both PPA and RSC responded significantly more to the walking videos compared to all other videos in both groups.

Occipital place area (OPA) still does not exhibit walking selectivity in 5-year-olds, even from their own perspective

Although the above findings demonstrate a lack of walking selectivity in the OPA of 5-year-olds, one alternative account still stands: is this lack of walking selectivity because the videos used above were taken from an adult walking perspective and

not from their own perspective? Perhaps the OPA in 5-year-olds will exhibit walking selectivity, but only from walking videos from their own perspective. To directly address this possibility, we scanned a new group of 5-year-olds with videos taken from 5-year-old walkers (see Methods). As shown in Fig. 5A, OPA in 5-year-olds still does not respond to the 5-year-old perspective walking videos any more than to the crawling or flying ones. Indeed, a 4-level (walking, crawling, flying, and scrambled) repeated-measures ANOVA revealed a significant main effect ($F(3,27) = 6.04$, $P = 0.003$, $\eta_p^2 = 0.40$), with a significantly greater response to each of the walking, crawling, and flying videos compared to the scrambled ones (all P 's < 0.017), but no significant differences between the walking, crawling, and flying videos (all P 's > 0.126). Thus, even when 5-year-olds are watching videos from their own perspective, OPA still does not exhibit walking selectivity. Next, we compared the responses in OPA to the 5-year-old perspective videos to the adult perspective videos. A 2 (walking perspective: adult, 5-year-old) \times 4 (condition: walking, crawling, flying, scrambled) mixed-model ANOVA revealed no significant

interaction ($F(1.85, 48.18) = 1.82$, $P = 0.18$, $\eta_p^2 = 0.07$) demonstrating that the response in OPA did not differ between the adult and 5-year-old walking perspectives (see Figs. 4A and 5A).

This lack of walking selectivity in OPA cannot be explained by motion differences across the 5-year-old perspective videos. Indeed, a 2 (ROI: OPA, MT) \times 4 (condition: walking, crawling, flying, scrambled) mixed-model ANOVA revealed a significant ROI by condition interaction ($F(3, 27) = 5.542$, $P = 0.004$, $\eta_p^2 = 0.381$; Fig. 5A and B). Finally, the lack of walking selectivity in OPA is specific to OPA. Indeed, a 2 ROI (OPA, PPA, or RSC) \times 4 (condition: walking, crawling, flying, scrambled) mixed-model ANOVA revealed a significant group by ROI by condition interaction for both OPA and PPA ($F(3, 27) = 4.895$, $P = 0.008$, $\eta_p^2 = 0.352$; Fig. 5A and C) and OPA and RSC ($F(3, 27) = 5.213$, $P = 0.006$, $\eta_p^2 = 0.367$; Fig. 5A and D).

Is the late development of the occipital place area (OPA) experience-dependent or simply maturational?

Previous research has demonstrated that children achieve adult-like walking skills later in childhood, around 8 years of age (Pryde et al. 1997; Berard and Vallis 2006; Michel et al. 2010), coinciding with the late emergence of walking selectivity in OPA, which suggests a possibility that neural responses in OPA are related to children's navigation behaviors. To directly explore this possibility, we conducted a behavioral experiment, where we asked children to judge the navigational perspective (i.e. "walking" or "crawling") from the videos.

As shown in Fig. 6, the 5-year-olds were significantly worse at judging navigational perspective (i.e. walking versus crawling) than were the 8-year-olds ($t(15.40) = 6.249$, $P < 0.001$; see Fig. 6A). Critically, the 5-year-olds and the 8-year-olds performed similarly on a control task ($t(14.33) = 1.361$, $P = 0.194$; Fig. 6B below), where they were asked to judge whether the video depicted an inside or outside setting, revealing that the 5-year-olds were paying attention to the videos. Furthermore, when directly comparing the response in OPA to the walking videos and the 5-year-olds' performance on the behavioral task, we observed a significant positive correlation (see Fig. 6C below; $r = 0.638$, $P < 0.01$). Critically, this significant correlation was only observed in OPA; there was no significant correlation between the response in PPA to the walking videos and task performance (see Fig. 6D below; $r = 0.09$, $P = 0.739$). Finally, given that 8-year-olds' task performance was near the ceiling, we did not expect to observe a meaningful correlation between the response in OPA (or PPA) and task in 8-year-olds. Nevertheless, we still examined this relationship in 8-year-olds for completeness and indeed found no significant correlation between the response in OPA to the walking videos and task performance ($r = 0.166$, $P = 0.569$; Fig. 6E) nor a significant correlation between the response in PPA to the walking videos and task performance ($r = -0.304$, $P = 0.289$; Fig. 6F). Note, however, that with a more challenging task, one may still observe a significant relationship between the response in OPA and behavior in 8-year-olds, which obviously requires additional research.

So, what cortical system then supports walking in 5-year-olds?

If OPA does not represent visual information about walking in 5-year-olds, then which cortical system does—after all, children at this age are most definitely walking? To address this question, we performed a group-level whole-brain analysis to find regions that respond more to the walking videos than to the crawling, flying, or scrambled ones using a conjunction contrast (i.e. walking > crawling and walking > flying and walking > scrambled). For

this analysis, we combined the data where children watched the videos from the adult perspective with the data where children watched the videos from the 5-year-old perspective, since OPA in the 5-year-olds showed a similar pattern of response in both perspectives. As shown in Fig. 7, this analysis revealed two regions (i.e. PPA and RSC), raising the intriguing possibility that either PPA or RSC, or both, may support walking in young children until OPA reaches full maturity—which is a likely possibility as some evidence suggests that PPA and RSC develop earlier than OPA (Kosakowski et al. 2022). Note, however, that this finding needs to be interpreted with caution, since the greater responses in PPA and RSC to the walking perspective may simply be due to the greater amount of scene information in the walking videos compared to other videos (Jones et al. 2023), especially given that both PPA and RSC did not exhibit the walking selectivity (Fig. 4). Thus, future research is needed to fully investigate this possibility.

How is crawling supported in the developing brain?

Our findings demonstrate that OPA does not represent visual information about crawling in either 5-year-olds or 8-year-olds (Fig. 2A), consistent with a recent fMRI study in adults (Jones et al. 2023). Instead, Jones et al. (2023) found regions in the inferior and superior posterior lobules that responded significantly more to the crawling videos than to the walking, flying, and scrambled ones, suggesting that crawling may be supported by these cortical regions. Similarly, using a group-level whole-brain and conjunction analysis, we found that the inferior parietal lobule responds significantly more to the crawling videos than to the walking, flying, and scrambled ones in both 8-year-olds and 5-year-olds (Fig. 8). Given these consistent findings across 5-year-olds, 8-year-olds, and adults, the inferior parietal lobule, not OPA, may support crawling and early navigation behaviors in crawling infants.

Discussion

In this study, we investigated when walking selectivity in OPA emerges in development. We found that OPA in 8-year-olds, like adults, exhibits walking selectivity—that is, representing visual information from a walking perspective only, not from a crawling, flying, or scrambled perspective. By contrast, in 5-year-olds, OPA does not show walking selectivity at all—responding not differently to the walking videos than to the crawling or flying ones. Importantly, these different patterns of response in OPA between 5-year-olds and 8-year-olds were not due to differences in data quality, scene selectivity, motion processing, attention, or walking perspective.

Our findings support the hypothesis that OPA undergoes protracted development, supporting visually guided navigation via walking, not crawling (Jones et al. 2023). Furthermore, and importantly, our findings extend this hypothesis and suggest that OPA only supports walking late in childhood, around 8 years of age, and not beforehand. This refined hypothesis dovetails with several behavioral studies showing that it takes around 8 years for children to master adult-like walking, as previously discussed (Pryde et al. 1997; Berard and Vallis 2006; Michel et al. 2010), and to use peripheral cues during navigation like adults (Franchak et al. 2010). Moreover, a recent fMRI study (Kamps et al. 2020) showed that OPA is not even sensitive to motion information in scenes in children 5 years of age, and this sensitivity in OPA only emerges in children around 8 years of age, further supporting the hypothesis that OPA develops late in childhood, again, around 8 years of age.

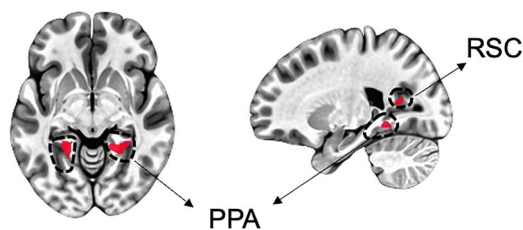


Fig. 7. A group-level whole-brain analysis in the 5-year-old revealed two clusters showing a significantly greater response to the walking videos than to the crawling, flying, and scrambled ones ($P < 0.05$, cluster-based multiple comparison correction with voxel size >295). These clusters are found where PPA and RSC are located (the location of the parcel PPA/OPA is noted with dashed lines), respectively, which is consistent with the ROI-based analyses.

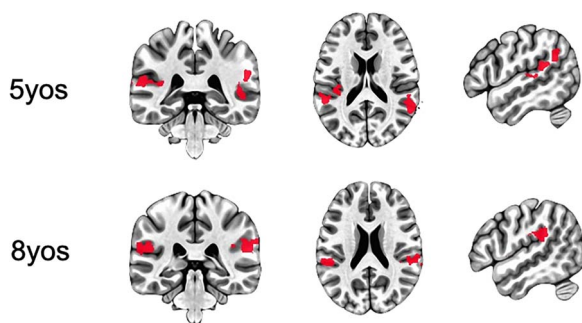


Fig. 8. Group-level whole-brain analyses revealed brain regions, located in the inferior parietal lobule (IPS), showing a significantly greater response to the crawling videos than to the walking, flying, and scrambled videos ($P < 0.05$; cluster-based multiple comparison correction at voxel size >295) in 5-year-old and 8-year-old children, labeled accordingly.

But what is required for the development of OPA? One possibility is that extensive experience with walking is necessary for OPA development. As discussed earlier, children achieve adult-like walking abilities later in childhood (Pryde et al. 1997; Berard and Vallis 2006; Michel et al. 2010), coinciding with the late emergence of walking selectivity in OPA. This finding suggests that walking experience from toddlerhood to later in childhood may contribute to OPA development. If this is the case, we might observe earlier OPA development in younger children with extensive walking experience. Indeed, the finding from the behavioral experiment supports this possibility by revealing that OPA's responses to the walking videos are related to children's spatial cognitive ability (i.e. the ability to distinguish different navigational perspectives). Another possibility, however, is that OPA undergoes protracted development regardless of the amount of walking experience. Supporting this idea, studies have indicated slower maturation in the dorsal stream of the cortex (Braddick et al. 2003; Atkinson and Braddick 2011), where OPA is located (Dilks et al. 2011, 2013). As our current study did not control for the amount of walking experience across the two age groups, it remains unclear whether OPA development is experience-driven or maturational, which is an interesting avenue for future research.

How are early navigational behaviors, including early walking, supported? Indeed, beyond the pure observation that children before 8 years of age can walk around, several studies have indicated that some of the important navigation-related skills, including reorientation (Hermer and Spelke 1994) or depth perception (Gibson and Walk 1960), emerge early in childhood, by 2–3 years of age. One possibility, then, is that such early navigational behaviors are supported by another, earlier-developing system.

For example, as suggested here, early walking may be supported by other scene-selective regions, like PPA or RSC, as the scene selectivity in these regions appears to develop earlier than OPA in infancy (Kosakowski et al. 2022). Indeed, in adulthood, RSC even represents navigationally-relevant information, such as distance (near or far; Persichetti and Dilks 2016) and sense (left or right; Dilks et al. 2011)—like OPA. Therefore, it is possible that RSC, but not OPA, represents such navigationally-relevant information in young children and supports these early navigational behaviors in children. If this is the case, then OPA may discontinuously develop and hence not be involved in visually guided navigation at all until children are around 8 years of age.

By contrast, it is also possible that OPA develops continuously and supports early navigational behaviors with a primitive and limited capacity, even early on. Supporting this possibility, OPA in 5-year-olds shows scene selectivity just like older children, as shown here (also see Kamps et al. 2020), and thus such early emerging scene selectivity in OPA may be sufficient to support early navigational behaviors, which in turn could guide further refinement of later emerging properties (e.g. walking selectivity) in OPA. If this is the case, OPA may represent some of the primitive kinds of information required for visually guided navigation, such as distance or sense, in young children, which is an ample avenue for future research.

Finally, how is crawling supported in the developing brain? Consistent with the previous finding in adults (Jones et al. 2023), we found that OPA in both groups of children does not represent crawling (Fig. 4A), showing a similar response to the crawling videos and to the flying videos, which depicts a perspective that humans do not experience during navigation. Similar to adults, we found that the inferior parietal lobes represent visual information from crawling, showing a greater response to crawling than walking, flying, or scrambled, in both groups of children (Fig. 8). As these regions are shown to be involved in reaching and grasping (Cavina-Pratesi et al. 2018), and since crawling involves moving the arms, it is reasonable to hypothesize that the inferior parietal lobe supports crawling behavior. Note, however, that future studies on crawling infants are needed to further explore this possibility.

In conclusion, we found that walking selectivity in OPA is not even present in children 5 years of age and instead only emerges in children around 8 years of age. These findings suggest that the development of visually guided navigation is surprisingly late, not fully developed until around 8 years of age, when children become “adult” walkers.

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Authors' contribution

Yaelan Jung (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing—original draft, Writing—review & editing), Debbie Hsu (Investigation), and Daniel Dilks (Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing—review & editing).

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