# The Development of Human Cortical Scene Processing

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## Abstract

Decades of research have uncovered the neural basis of place (or "scene") processing in adulthood, revealing a set of three regions that respond selectively to visual scene information, each hypothesized to support distinct functions within scene processing (e.g., recognizing a particular kind of place versus navigating through it). Despite this considerable progress, surprisingly little is known about how these cortical regions develop. Here we review the limited evidence to date, highlighting the first few studies exploring the origins of cortical scene processing in infancy and the several studies addressing when the scene regions reach full maturity, unfortunately with inconsistent findings. This inconsistency likely stems from common pitfalls in pediatric functional magnetic resonance imaging, and accordingly, we discuss how these pitfalls may be avoided. Furthermore, we point out that almost all studies to date have focused only on general scene selectivity and argue that greater insight could be gleaned by instead exploring the more distinct functions of each region as well as their connectivity. Finally, with this last point in mind, we offer a novel hypothesis that scene regions supporting navigation (including the occipital place area and retrosplenial complex) mature later than those supporting scene categorization (including the parahippocampal place area).

## Keywords

scene recognition, navigation, pediatric fMRI, PPA, OPA, RSC

Research in the past three decades has significantly advanced our understanding of adult human scene processing, uncovering a network of three "scene-selective" brain regions: the parahippocampal place area (PPA; Epstein & Kanwisher, 1998), the occipital place area (OPA; Dilks et al., 2013), and the retrosplenial complex (RSC; Maguire, 2001). These regions are so-called scene selective because they each respond about 2 to 4 times more to images of scenes than objects, faces, and other categories—but, interestingly, differ in the particular function each plays *within* scene processing. Specifically, we recently proposed that PPA supports our ability to recognize a scene as a particular kind of place (*scene categorization*), OPA supports our ability to navigate through the immediately visible place (*visually guided navigation*), and RSC supports our ability to navigate through the broader environment (*map-based navigation*; Dilks et al., 2022; Fig. 1).

But how does cortical scene processing develop? To gain initial traction on this question, the earliest

studies—in fact, nearly all studies to date—have focused on scene selectivity. This approach has not been without success. For example, it is now clear that at a minimum, scene selectivity is detectable in children and even infants. At the same time, however, this approach faces challenges. For example, the field (a) is currently rife with inconsistent findings without clear standards for addressing the methodological pitfalls of pediatric functional magnetic resonance imaging (fMRI) that likely caused them and (b) has not yet produced any specific hypotheses to test.

Here we review what we have learned so far about the development of cortical scene processing and offer suggestions for a path forward. First, we point out the methodological pitfalls of pediatric fMRI and suggest ways in which they can be addressed. Second, we argue

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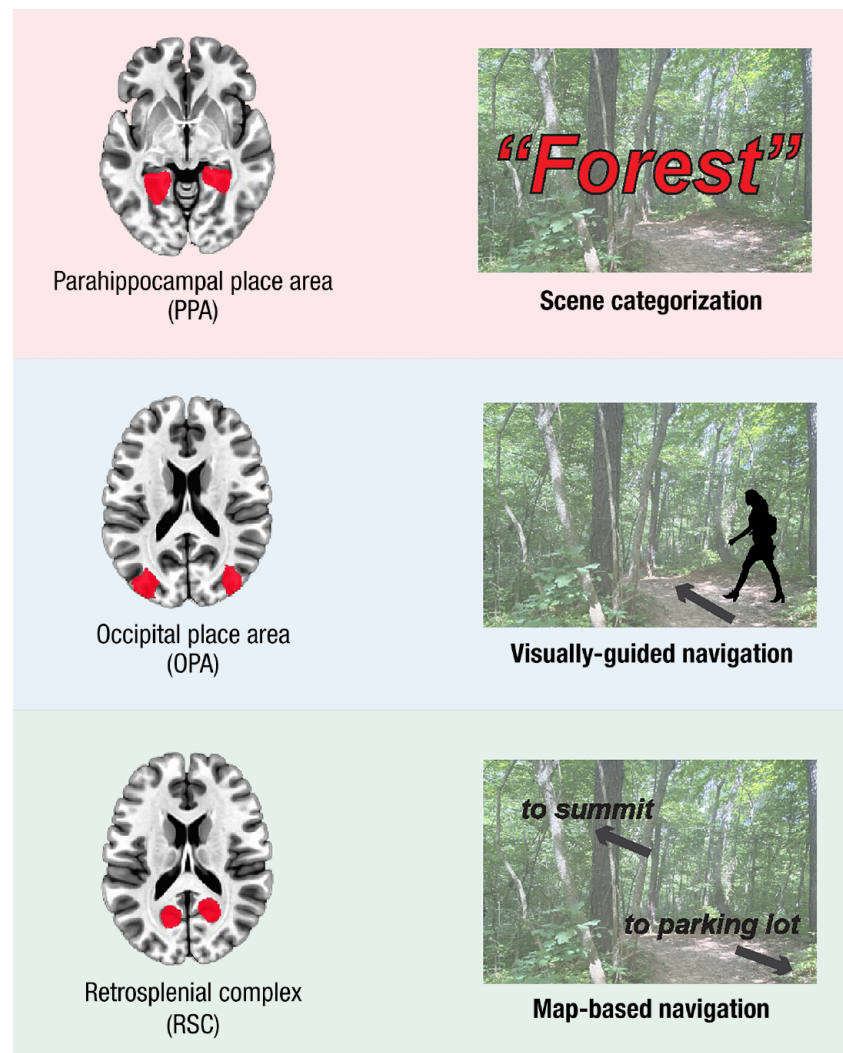Email: dilks@emory.edu

**Fig. 1.** The scene-selective regions (left panel) and their distinct scene processing functions (right panel). The parahippocampal place area supports scene categorization, our ability to recognize a scene as a particular kind of place (e.g., a forest not a kitchen). The occipital place area supports visually guided navigation, our ability to find our way through the immediately visible place, avoiding boundaries and obstacles (e.g., the trees and boulders on a trail). The retrosplenial complex supports map-based navigation, our ability to find our way from a specific place to a distant, out-of-sight place (e.g., from the trail to the summit or parking lot).

that serious progress in understanding the development of cortical scene processing will require moving beyond the current focus on scene selectivity and instead characterizing how the particular function of each region develops. Third, we emphasize that a deeper understanding of the connectivity profile of the scene regions can significantly expand our knowledge of the development of cortical scene processing. Fourth, and finally, building on these suggestions, we propose a new developmental theory: that each scene region develops along a different timeline, with both the visually guided and map-based navigation systems (including OPA and RSC,

respectively) developing later than the scene categorization system (including PPA). Note that some of these topics have been discussed in our recent review on the three cortical scene systems and their development (Dilks et al., 2022), but in the current article, we focus and expand our discussion on the development of the three systems.

## How Does Scene Selectivity Develop?

Two studies (Deen et al., 2017; Kosakowski et al., 2022) so far have investigated when scene selectivity can first

be detected in the infant brain. Using techniques designed to improve the quality and quantity of awake infant fMRI data, including infant-sized 32-channel head coils (Ghotra et al., 2021; Keil et al., 2011) and dynamic and engaging stimuli (Pitcher et al., 2011), these studies show that by just 4 to 5 months of age, all three regions show a basic "preferential" response to scenes (i.e., responding significantly more to scenes than at least one category, faces), but only one of these regions—PPA—responds selectively to scenes versus all other categories. Critically, infant PPA responses were not predicted by low-level visual features (i.e., eccentricity, spatial frequency, and rectilinearity; Kosakowski et al., 2022), challenging dominant theories of cortical development that emphasize the role of low-level visual statistics only in scaffolding later development (Arcaro & Livingstone, 2021). This initial work therefore suggests that PPA is present as early in development as we can yet measure and either is innately determined or requires only a few months of visual experience, whereas scene selectivity in OPA and RSC may emerge later (a point that will be discussed in more detail).

But are scene-selective responses already adultlike in infancy, or do they continue to develop across childhood? The evidence so far is remarkably inconsistent. For example, some studies found no change in selectivity between children and adults (Jiang et al., 2014; Scherf et al., 2007, 2011; Vuontela et al., 2013)—hence, suggesting that PPA is fully mature by at least 7 years of age—whereas two other studies revealed significant increases in selectivity between childhood and adulthood (Golarai et al., 2007; Meissner et al., 2019), suggesting that PPA does not reach full maturity until adolescence. This lack of consensus is not limited to PPA. For RSC, one study (Meissner et al., 2019) suggested that RSC is adultlike by 7 years old, whereas another study (Jiang et al., 2014) found weaker responses in 7-year-olds than in adults. For OPA, the only study comparing children and adults directly found weaker scene selectivity in children 7 years of age (Meissner et al., 2019).

What explains these inconsistent findings? One likely culprit is data quality: Because children move their heads more and pay less attention, children produce lower-quality data on average than adults (McKone et al., 2012), adding noise to estimates, generating spurious findings within a study, and consequently exacerbating inconsistent results across studies. Despite increasing attention to this issue, however, the field still does not yet have any widely used standards to rigorously address these confounds, and all studies to date in this small literature fall prey to at least one of the pitfalls of pediatric fMRI discussed next. The challenge is not insurmountable, though, and can be addressed

in the following ways: First, head motion confounds can be addressed by directly matching groups on head motion (e.g., see Meissner et al., 2019), ideally by using low-motion children only (rather than high-motion adults). Second, data quality confounds can be addressed by (a) matching groups on temporal signal-to-noise ratio (e.g., see Natu et al., 2016) and (b) using an individual region-of-interest (ROI) approach (Saxe et al., 2006). Third, attentional confounds can be addressed by (a) investigating "control" regions (e.g., to ensure children paid attention to visual stimuli, researchers can assess neural responses in V1; e.g., see Kamps, Pincus, et al., 2020), (b) using eye tracking (i.e., ensuring that participants were looking at the stimuli), and/or (c) matching performance between groups on a concurrent task (e.g., a one-back task).

Beyond data quality, other differences across studies could play a role as well. For example, the choice of control (or contrast) condition matters. For example, studies comparing scene responses to faces and objects (e.g., Scherf et al., 2011) may be more likely to observe scene selectivity early on, as compared with studies comparing scene responses to objects (e.g., Golarai et al., 2007), as the latter is a stricter test. Likewise, task demands could also play a role (e.g., passive viewing, as in Scherf et al., 2007, 2011, vs. one-back working memory tasks, as in Meissner et al., 2019, and Golarai et al., 2007), as children may pay less attention if the task is too challenging or not engaging enough. Finally, the choice of stimuli may also matter, because different kinds of scene stimuli may tap into different kinds of (more specific) scene information processing. For example, dynamic movies (e.g., as in Scherf et al., 2007, 2011) may emphasize visually guided navigation function, whereas static images (e.g., as in Golarai et al., 2007, and Meissner et al., 2019) may not. As there are only a few studies in this literature, it is not straightforward to point out which of these factors in particular contributed to the mixed results. Nonetheless, focusing only on very general measures of scene selectivity leaves us in a poor position for understanding the relative role of these factors. In the next section, we suggest a path forward for exploring the development of more specific information processing in scene selective cortex.

## Moving Beyond Scene Selectivity

Even if we determined once and for all how scene selectivity develops, would the question of how cortical scene processing develops be solved? We think not. Just as in adulthood, where understanding more specific functions has yielded clearer insights into adult cortical scene processing (compared with focusing on
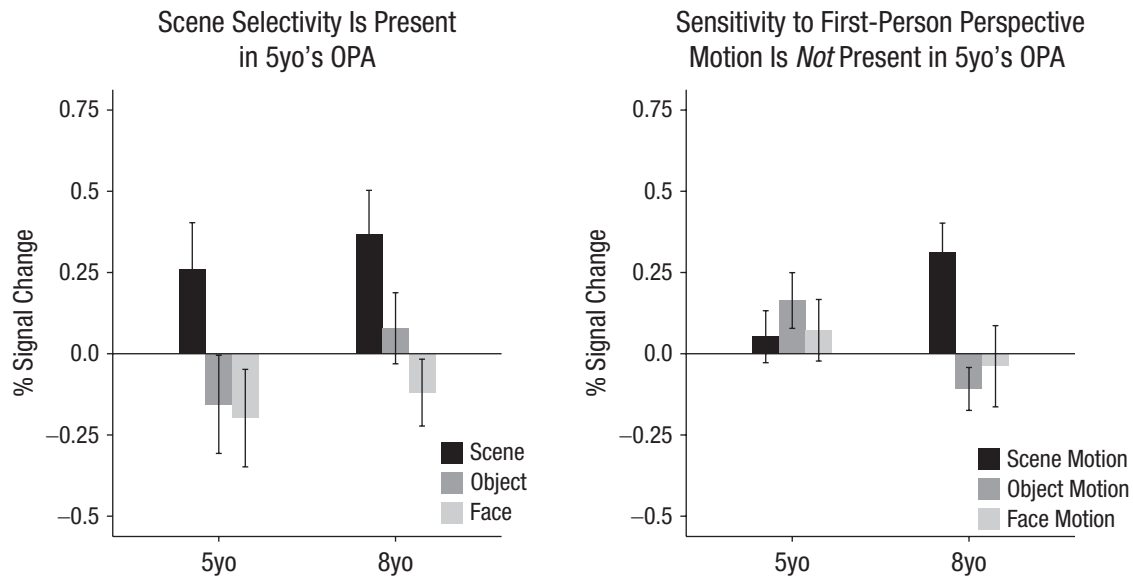
## Scene Selectivity Is Present in 5yo's OPA

## Sensitivity to First-Person Perspective Motion Is *Not* Present in 5yo's OPA



**Fig. 2.** When testing for scene selectivity using pictures of scenes, objects, and faces, the occipital place area (OPA) in both 5- and 8-year-olds showed a clear scene selective response (i.e., a greater response to scenes than the other categories; see the plot on the left). However, when testing functionally relevant information processing—in this case, first-person-perspective motion information (i.e., the response to scene videos, which have such motion information, minus that to static scene images)—OPA showed a clear developmental trend, responding only to this navigationally relevant motion information by age 8. Note that this trend was specific to scene motion and was not found for face or object motion, which do not drive responses in OPA of 8-year-olds. This developmental change was also specific to OPA and was not found in the parahippocampal place area, the retrosplenial complex, or early visual or motion-selective cortex.

scene selectivity alone), a full picture of how scene regions reach maturity must also account for these more specific functions. As a starting point, one might assume that more specific functions emerge in tandem with scene selectivity and therefore that scene selectivity should be a sufficient proxy for the overall maturity of a region. However, recent empirical evidence suggests this is not the case. Kamps, Pincus, et al. (2020) measured both scene selectivity (by comparing responses to scenes, objects, and faces) and first-person-perspective motion information processing (by comparing responses to dynamic scenes depicting this information with static images that did not; dynamic and static faces and objects were presented as control conditions)—a proxy for OPA's more specific function in visually guided navigation (Kamps et al., 2016). We found a clear developmental dissociation: Although OPA already exhibited scene selectivity in children 5 years of age that was not different from that in children 8 years of age, responses to first-person-perspective motion were not yet detectable by age 5 and did not emerge until age 8 (Fig. 2). Although these findings alone cannot rule out the possibility that earlier-emerging properties in OPA, including scene selectivity, support early navigation behaviors, these findings nonetheless indicate that general scene selectivity is not a sufficient

barometer for the more specific functions found in these regions by adulthood.

Additionally, by shifting focus to more specific functions rather than scene selectivity, we may gain clearer insight into how to link neural development with behavioral development. Indeed, it is not clear what specific behaviors should correlate with the development of general scene selectivity. By contrast, when considering more specific functions (e.g., visually guided navigation), the predictions become clearer. If OPA supports visually guided navigation and matures late in childhood, then we should also predict that children's visually guided navigation abilities to mature late in development. Consistent with this idea, a recent study investigated the development of spatial memory relative to boundaries using a task known to depend on OPA by adulthood (Julian et al., 2016) and found protracted development late into childhood (Julian et al., 2019). Furthermore, unlike adults, younger children are poorer at utilizing peripheral cues while navigating (Franchak & Adolph, 2010) and make more errors in obstacle avoidance and path-following tasks (Berard & Vallis, 2006). Thus, assessing the emergence of specific functions in each scene region will provide more specific predictions for other scene-related functions, including scene categorization and map-based navigation.

## Connectivity Can Also Tell Us About the Development of Scene Systems

Beyond measuring functional responses, another critical source of insight comes from studying how scene regions are connected, both to each other and to the rest of the brain. It is widely hypothesized that connectivity emerges earlier than function (e.g., Dubois et al., 2016; Saygin et al., 2016) and guides subsequent functional development. How early, then, does the connectivity of the cortical scene system emerge, and what role might it play in shaping functional development?

Most work has focused on the development of within-scene-network connectivity, using either resting-state fMRI or diffusion tensor imaging. By adulthood, scene regions show stronger connections to each other than to nearby regions engaged in other processes (e.g., face processing), with the exception of OPA and RSC, which are not strongly connected (Baldassano et al., 2013, 2016; Nasr et al., 2013). Recent evidence from neonates suggests that within-scene-network connectivity emerges within just 27 days of life (Kamps et al., 2020a). Specifically, regions in the neonate brain anatomically corresponding to PPA show stronger functional correlations to RSC than to nearby face regions. Such early-emerging within-scene-network connectivity could help sculpt scene network development, because regions that are wired up together from early on will be more likely to take on similar information processing (e.g., scene processing, not face processing). Other work has explored how within-scene-network connectivity matures later in childhood, revealing relative stability across childhood for the connection between PPA and RSC, along with protracted maturation of the connection between OPA and PPA (Meissner et al., 2021).

But how are scene regions connected to the rest of the brain? Importantly, although the within-scene-network connections just discussed can explain why scene regions take on similar information processing, they cannot explain why this network always takes on scene processing in particular rather than any other function (e.g., face processing)—or why each region takes on its more specific function within scene processing. One constraint may come from visual input: Given that scenes inherently extend across the entire peripheral visual field, scene regions may arise in regions that receive biased peripheral visual input (Arcaro et al., 2019). Consistent with this idea, neonate scene regions indeed show stronger functional connectivity with peripheral versus foveal early visual cortex (Kamps, Hendrix, et al., 2020). Another constraint may come from interactions with regions beyond the visual system. Indeed, neonate scene regions already show unique patterns of long-range connectivity (compared with nearby face regions; Cabral et al., 2022). An intriguing possibility then is that these "top-down" connections help constrain the more specific function each region takes on. For example, OPA may be connected to regions of parietal cortex (possibly supporting motor planning for visually guided navigation), whereas PPA may be connected to regions in the anterior and medial temporal lobe (possibly supporting semantic processing related to scene categorization; Baldassano et al., 2013, 2016; Nasr et al., 2013). Of course, differences between scene regions may arise from visual input as well. For example, work in adults shows that OPA and PPA have different biases toward the upper versus lower visual field (Silson et al., 2015), consistent with the idea that information from the low field is useful for navigation and the upper for categorization.

## A Novel Hypothesis: Visually Guided Navigation and Map-Based Navigation Develop Later Than Scene Categorization

Studies discussed so far reveal that the field has only begun to explore how cortical scene processing develops. What is more, this initial work has not yet provided any specific hypotheses regarding how each scene region develops, which are clearly needed to formulate and test theories of the development of cortical scene processing. Thus, here we offer a new hypothesis: that these systems develop along different timelines, with both navigation systems maturing later than the scene categorization system.

Although no pediatric fMRI studies have directly tested the hypothesis that the visually guided navigation system (including OPA) is slower to develop than the scene categorization system (including PPA), behavioral evidence supports this possibility. First, consider early infant visual experience: Typically developing infants are exposed to different places (e.g., living room or kitchen) before they can ever independently navigate around those places themselves. Second, analogous work in the object-processing literature shows that the "vision-for-action" (dorsal) system is slower to develop than the "vision-for-perception" (ventral) system (Atkinson et al., 2003; Dilks et al., 2008). For example, younger children are disproportionately less accurate in posting a card through an oriented slot (action) than in matching a card to the slot's orientation (Dilks et al., 2008). These results raise the possibility that different scene systems for action and recognition also follow the same, dissociable developmental trajectories. Third, and finally, the limited available evidence nevertheless supports the idea of protracted development of visually guided navigation. For example, as alluded to earlier,

navigation-related skills, including locomotion (Franchak & Adolph, 2010), obstacle avoidance (Berard & Vallis, 2006), and boundary-based spatial memory (Julian et al., 2019), appear to undergo protracted developmental trajectories, still developing as late as 8 years old. By contrast, scene recognition abilities appear early in life—even infants can recognize scene information (i.e., discriminating whether a cliff is deep or shallow) long before they can independently move around their surroundings (e.g., by crawling; Campos et al., 1970).

We further hypothesize that the map-based navigation system (including RSC) develops later than the scene categorization system. Again, this idea has not been directly tested yet with neuroimaging, but there is some promising behavioral evidence that supports this idea. That is, several behavioral studies have shown that map-based navigation ability—especially that relying on allocentric representations of the broader spatial environment—undergoes protracted development late into childhood (Newcombe, 2019). For instance, children's ability to learn about new routes and places in a virtual environment becomes adultlike around age 12 (Nazareth et al., 2018), which is no doubt much later than when children are initially exposed to different kinds of places (e.g., a kitchen or living room), beginning in infancy.

But what about the relative development of the visually guided versus map-based navigation systems? Do they develop along similar or different timelines? Given the proposal that these two systems are independent in adulthood (Dilks et al., 2022), it could be the case that they develop along different timelines as well. Future research is needed to address the development of these two systems.

## Conclusion

Here we review studies investigating what little is currently known about the development of human cortical scene processing. After discussing methodological pitfalls in this literature (and their remedies), we argue that a full account of the development of cortical scene regions will require moving beyond the current focus on scene selectivity to instead investigating the more specific functions of each region as well as their connectivity to each other and to other parts of cortex. Building on these suggestions, we then propose a novel hypothesis for future investigation: That is, the visually guided navigation system (including OPA) and the map-based navigation system (including RSC) are slower to develop than the scene categorization system (PPA).

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## Transparency

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