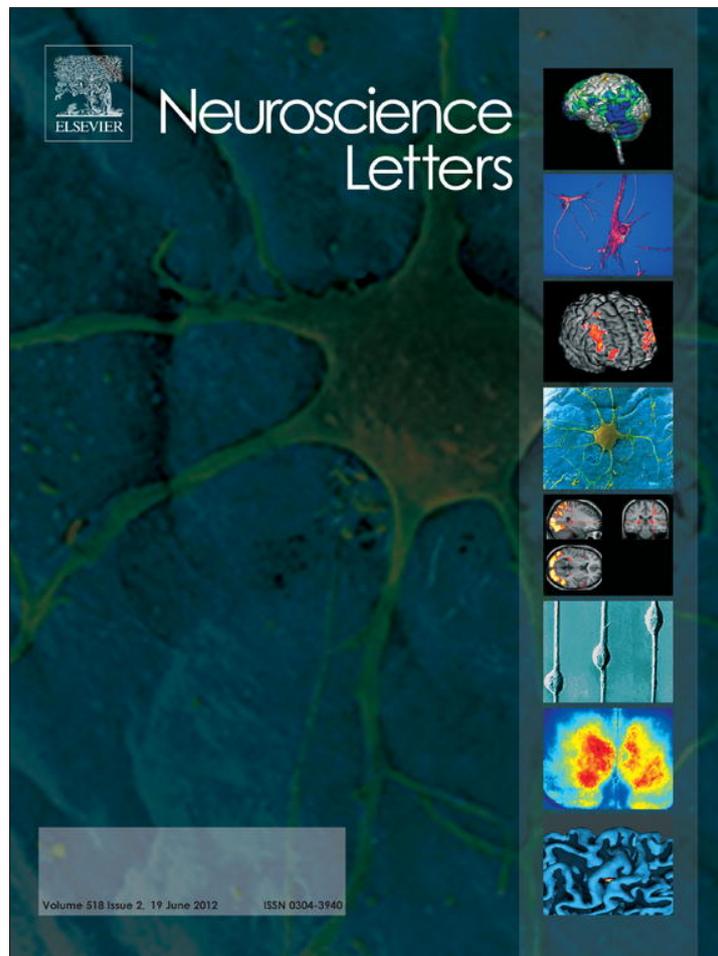


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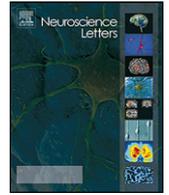
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Curious monkeys have increased gray matter density in the precuneus

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HIGHLIGHTS

- ▶ We examine the neural correlates of curiosity.
- ▶ Curious monkeys had a greater density of gray matter in the precuneus.
- ▶ The precuneus is associated with integrated tasks such as memory and self-awareness.
- ▶ Monitoring self-awareness may play a role in cognitive processes mediating curiosity.

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ABSTRACT

Curiosity is a cornerstone of cognition that has the potential to lead to innovations and increase the behavioral repertoire of individuals. A defining characteristic of curiosity is inquisitiveness directed toward novel objects. Species differences in innovative behavior and inquisitiveness have been linked to social complexity and neocortical size [18]. In this study, we observed behavioral actions among nine socially reared and socially housed capuchin monkeys in response to an unfamiliar object, a paradigm widely employed as a means to assess curiosity. *K*-means hierarchical clustering analysis of the behavioral responses revealed three monkeys engaged in significantly more exploratory behavior of the novel object than other monkeys. Using voxel-based-morphometry analysis of MRIs obtained from these same subjects, we demonstrated that the more curious monkeys had significantly greater gray matter density in the precuneus, a cortical region involved in highly integrated processes including memory and self-awareness. These results linking variation in precuneus gray matter volume to exploratory behavior suggest that monitoring states of self-awareness may play a role in cognitive processes mediating individual curiosity.

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1. Introduction

Curiosity is the desire to learn about what is unknown. Montgomery [15,16] postulated that human and animal behavior is often motivated by such self-enrichment tendencies. His approach-avoidance theory maintained that curiosity is a balance between two motivations—the drive to explore and the fear resulting from the novel situation. Berlyne [5] considered curiosity to be a motivational drive, and a prerequisite for exploratory behavior. The motivation for curiosity is unique from other drives in that it is aroused not by an internal state in the individual, but rather by a novel external stimulus. This motivation is also satiated quickly with continuous exposure to the stimulus.

Curiosity and exploratory behavior are intertwined and as such, difficult to define independently; both terms are used to refer to behavior that provides a gain in information about the environment.

The neurobiology underlying curiosity remains poorly understood. In humans, curiosity has been linked to functional activation in the inferior frontal gyrus (Broca's area) and the caudate nucleus, associated with anticipated reward [13]. Dopaminergic receptors in the dentate gyrus are associated with the generation of exploratory behavior in mice [20]; these receptors also play a role in learning and memory.

Here, we characterized behavioral responses among nine socially reared and socially housed capuchin monkeys to a novel object, a paradigm widely employed as a means to assess curiosity [8,17,25]. Additionally, we obtained high-resolution T1-weighted structural magnetic resonance images of the brain from these same monkeys, to relate neuroanatomical differences to their behavior.

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Fig. 1. Still images illustrating an individual monkey engaging in tactile exploration (a) and olfactory and visual exploration (b).

2. Materials and method

2.1. Subjects

Nine adult capuchin monkeys (*Cebus apella*) were used in this study, including five males and four females ranging in age from 5 to 23 years ($M=13.4$ years, $SD=6.6$ years). Subjects were socially housed in enriched environments with perches, swings, and fresh browse. The social composition of this group closely resembled that of wild groups; furthermore, normative capuchin social behavior—including grooming and playing—was regularly displayed. New World Monkey Chow and water were available *ad libitum*; fruit was provided once a day. This study was carried out in strict accordance with the recommendations in the Guide for the Care and Use of Laboratory Animals of the National Institutes of Health and was approved by the Institutional Animal Care and Use Committee, Hiram College, Hiram Ohio, USA.

2.2. Behavioral testing

All subjects were removed from the social group and tested individually in a separate enclosure ($1.5\text{ m} \times 1.5\text{ m} \times 2.4\text{ m}$), without a human present. All were familiar with the enclosure from participation in a prior experiment on prey capture behavior [10]. Monkeys remained in the enclosure for 5 min, where they had no auditory or visual contact with other monkeys or humans. Behavioral responses were scored from video recordings made of the testing session. The enclosure had a Plexiglas panel on the front portion through which unobstructed visual access was provided. Before a trial began, a brightly colored, novel object was hung on a wall on the inside of the enclosure (Developlay Activity Center by Tiny Love). This children's toy has several objects that can be manipulated through pulling, pushing, turning, etc. Different textures, sounds, and colors enhance the novelty and feedback responsiveness of the object. A perch was positioned beneath the object to provide access to subjects.

A video camera was positioned on a tripod to provide an unobstructed view of the perch and object. A trial began once a subject was transferred into the testing enclosure. During trials, the

experimenter was not in the room and was no longer in visual or auditory contact with the subject. The subject was allowed to explore the novel object for 5 min. After 5 min the experimenter returned to the room and turned off the video camera; the subject was transferred out of the testing enclosure and returned to the social group. Each subject received one trial.

2.3. Image acquisition

Structural MRIs of the brain were obtained from subjects separately from the behavioral testing session. In order to obtain the noninvasive MRI images required for this study, the subject's head needed to be immobile during the scan. Therefore, the capuchins were anesthetized for the procedure. Anesthesia was used only for the purpose of restraint during collection of the brain images. Subjects remained anesthetized throughout the MRI procedure and respiration rate, heart rate, and oxygen consumption were continually monitored by a veterinarian.

In vivo structural magnetic resonance scans were obtained for all subjects on a Siemens 3.0 Tesla Scanner at the Neuroscience Imaging Center in Pittsburgh, PA. Subjects were initially immobilized by ketamine (7 mg/kg) and medetomidine (0.06 mg/kg) injection and subsequently anesthetized with propofol (250–350 $\mu\text{g}/\text{kg}/\text{min}$). Subjects were then placed into the scanner chamber and their heads were fitted inside a 12 cm head coil. High-resolution (isotropic 0.5 mm) T1-weighted 3D MPRAGE scans were acquired ($TR=1500$ ms, $TE=3.04$ ms, no echo-train, number of signals averaged=3, matrix size=256 \times 256). Scan acquisition time was approximately 50 min. After completing the MRI procedure subjects were allowed to recover from the effects of anesthesia before return transport.

Prior to analysis, data were converted into the Nifti file format. Nifti files for individual subjects were numerically coded prior to analysis to prevent observer bias.

3. Results

Video recordings of the test session were scored by an individual who was unfamiliar with the subjects. The following data were

Table 1

Individual subject data, including sex, age, grouping (curious or less-curious), latency to first approach the novel object, and the total number of tactile, olfactory and visual exploratory behaviors demonstrated by each individual during the 5 min testing session.

Name	Sex	Age	Latency ^a (s)	Tactile	Olfactory	Visual	Grouping
Carlos	M	8	6	2	0	10	Curious
Dee	F	23	65	1	3	1	Less-curious
Ellie	F	17	9	0	2	7	Curious
Georgia	F	9	126	0	1	5	Less-curious
Miro	M	15	10	0	0	9	Curious
Noel	F	17	12	0	1	5	Less-curious
Shoeless	M	5	296	0	1	1	Less-curious
Sosa	M	6	286	0	0	5	Less-curious
Vincent	M	21	22	1	2	2	Less-curious

^a Latency corresponds to time to first approach in seconds.

recorded for each subject: latency to first approach the object and the total number of exploratory actions of different types during the 5-min testing session. [A complete description of the scoring procedure can be found in Supplement.] Exploratory behavior toward the object consisted of any of the following behaviors:

- tactile exploration—touching, grabbing, climbing upon, or rubbing (with body or limb) the object (see Fig. 1a);
- olfactory exploration—putting the nose or face in close proximity to the object (see Fig. 1b);
- oral exploration—licking or mouthing any portion of the object; and
- visual inspection—approaching the object and looking closely at any part of the object; may co-occur with other types of exploration (see Fig. 1b).

During the test sessions, monkeys engaged in tactile, olfactory, and visual inspection (Table 1); though all monkeys predominantly used close visual inspection as compared to the other modes of exploration. The number of times that each monkey performed these three action types was entered into a *k*-means clustering algorithm to define two distinct groups—the more curious monkeys and the less curious monkeys (see Fig. 2). After the *k*-means clustering analysis sorted the subjects into these two groups, then Euclidean distance metrics were used to assign subjects within clusters based on the total data from the behavioral task. The “curious” group was comprised of three monkeys that performed a mean of 10 actions ($SD = 1.73$) on the novel object during the testing period. The “less-curious” group was comprised of six monkeys that performed a mean of 4.83 actions ($SD = 1.47$). The difference in total number of actions performed by the curious and less curious monkeys was statistically significant (Mann–Whitney *U*, $z = -2.384$, $p = 0.017$). The latency to approach the novel object was also significantly shorter for the curious monkeys ($M = 7$ s; $SD = 1$ s) than the less curious monkeys ($M = 48.7$ s; $SD = 24.9$ s; Mann–Whitney *U*, $z = -2.324$, $p = 0.024$).

These two categories of subjects were then used as the independent grouping variable for comparison of brain gray matter density differences across the entire brain. Structural MRI data were analyzed with FSL-VBM, a voxel-based morphometry (VBM) style analysis [3,9] carried out with FSL tools [23]. VBM allows for the investigation of voxel-wise differences in the gray matter volume between groups of subjects (*i.e.*, curious monkeys and less curious monkeys). This is an unbiased approach, as it requires no *a priori* information about the brain locations of possible differences in gray matter. Structural images were first brain-extracted using BET [22]. Next, tissue-type segmentation was carried out using FAST4 [26]. The resulting gray-matter partial volume images were then aligned to a capuchin standard brain space using the affine registration tool FLIRT [11,12], followed by nonlinear registration using FNIRT [1,2],

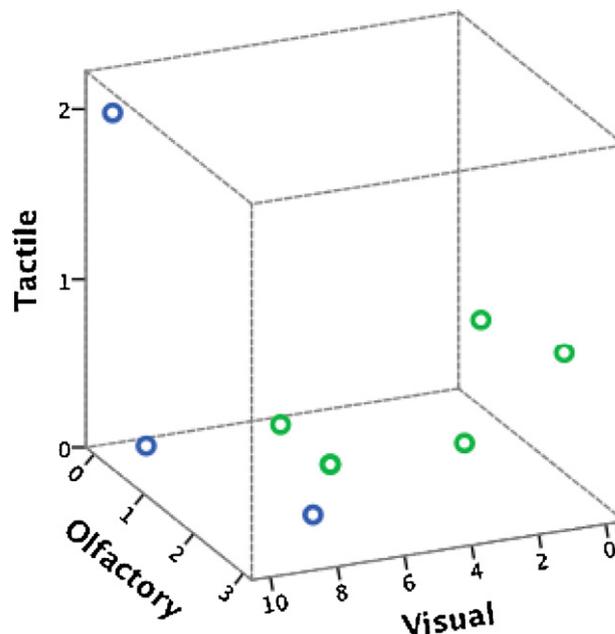


Fig. 2. A 3D scatterplot showing the number of exploratory actions by category (tactile, olfactory, and visual exploration) by each individual. Curious monkeys are grouped as blue; less curious monkeys are grouped as green.

which uses a b-spline representation of the registration warp field [19]. The resulting images were averaged to create a study-specific template, to which the native gray matter images were then non-linearly re-registered. The registered partial volume images were then modulated to correct for local expansion or contraction by dividing by the Jacobian of the warp field. The modulated segmented images were then smoothed with an isotropic Gaussian kernel with a sigma of 3 mm. Voxelwise GLM was applied using permutation-based non-parametric testing, correcting for multiple comparisons across space. We used threshold-free cluster enhancement (TFCE), a statistical method whereby one does not have to define initial cluster-forming threshold (which is arbitrary) or carry out a large amount of data smoothing [24].

Results of the VBM indicated significant differences (corrected *p* value < 0.05) in gray matter density between curious and less-curious monkeys in the cortical region of the precuneus of the left hemisphere (see Fig. 3). Curious monkeys displayed a greater gray

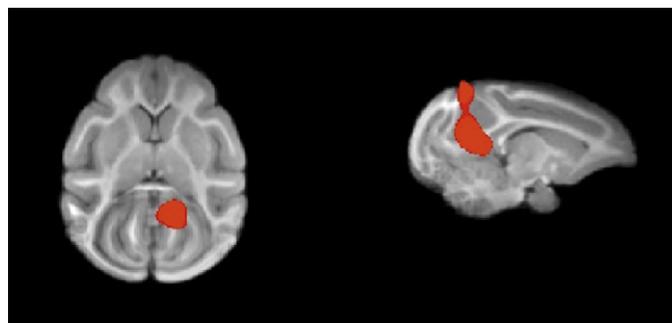


Fig. 3. Statistical parametric map showing brain regions with significant increase (red colored) in gray matter density in curious monkeys compared with less curious monkeys. Curious monkeys showed greater density of gray matter in the precuneus of the left hemisphere. In the axial section the right of the image is the left side of the brain.

matter density in the precuneus. No other brain areas revealed significant differences in gray matter density.

4. Discussion

In the current study, highly curious monkeys had a greater density of gray matter in the precuneus than the less curious monkeys. To our knowledge, this is the first investigation concerning the neural basis of variation in curiosity amongst individuals, and the first investigation to indicate that the precuneus is involved in curiosity. The precuneus plays a central role in highly integrated tasks in humans including episodic and semantic memory, and self-awareness [6,7]. Our results suggest that the precuneus also plays a role in exploratory behavior associated with curiosity; specifically, monitoring states of self-awareness may play a role in cognitive processes mediating individual curiosity. Because early environmental experiences affect animal curiosity [14,21], it is important to note that all of the capuchins tested in the present study were socially reared with their mother and socially housed in enriched environments. Thus, the observed differences in curiosity cannot be explained by differences in rearing history. Furthermore, as both the curious and less curious groups contained both males and females, and adults and juveniles, it does not seem that the results were influenced by these factors. However, as these factors could be reasonably expected to influence the expression of curiosity, further research should address this question.

Our results indicate that gray matter density of the precuneus is associated with individual variation in curious behavior. The precuneus of capuchin monkeys (*C. apella*) has been demonstrated to have reciprocal projections to widespread regions of the cortex, characterized by strong interconnectivity to the adjacent retrosplenial and posterior cingulate cortices [7]. These connections of the precuneus allow for the integration of self-generated information and external stimuli in a system that provides positive reinforcement for the acquisition of skills and knowledge. The dentate gyrus, part of the hippocampal formation, may contribute to the formation of new memories. In mice, dopaminergic receptors in this region were also associated with synaptic plasticity and memory acquisition [20]. Additionally, curiosity may enhance memory for surprising new information in reference to what is already known [13]. The striatum has projections to the precuneus [7]; striatal activity could be due to increased attention, resulting in an individual being more attentive to an object that is rewarding.

Species differences exist in the propensity to be curious. Torigoe [25] tested 74 primate species in their responsiveness toward novel stimuli. While a large degree of inter-specific variability was observed, apes, macaques, and capuchin monkeys – all large-brained, socially complex primates – were the most actively responsive to the objects. Behavioral innovation and executive brain ratio are positively correlated [18] and neocortical evolution has been related to the cognitive demands of sociality [4]. One interpretation concerns the importance of processing visual information and the parallel processing of topographically organized visual, tactile and auditory information. Such processing of sensory stimuli combined with relevant social information, likely involves a tremendous amount of sensory and cognitive integration which must be monitored in reference to states of self-awareness. The fact that curious monkeys had greater gray density of the precuneus is consistent with this interpretation. In the future, it will be important to determine whether phylogenetic variation in the morphology, connectivity, or gene expression of the precuneus can be related to species differences in exploratory behavior and innovation rate.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.neulet.2012.05.004>.

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