An emotional response is multidimensional, with perceptual, expressive, and subjective components. These responses can be attributed both to factors that are developmental or “ontogenetic” as well as to factors that are innate or “phylogenetic” (Mühlberger, Wiedemann, Herrmann, & Pauli, 2006). Ontogenetic emotional reactions often stem from associative learning or evaluative conditioning, processes that lead to the formation of likes and dislikes. These learned reactions can arise from firsthand experience (De Houwer, Thomas, & Baeyens, 2001) or because a third party has instructed the learner about the importance of a stimulus (Phelps et al., 2001). Phylogenetic emotional reactions may instead be hard-wired in the brain or may result from learning mechanisms that have been preserved across the course of evolution. For instance, human infants and monkeys will quickly learn to startle at the sight of a snake (DeLoache & LoBue, 2008; Ohman & Mineka, 2001), and rats may be born with fight-or-flight mechanisms triggered by odors of predators that they have never before encountered (Kobayakawa et al., 2007).

Although the behavioral manifestations of the responses elicited by ontogenetic and phylogenetic stimuli appear similar, there is some evidence to suggest that the neurobiological mechanisms yielding those responses may be different. For example, a rat’s freezing behavior in response to a conditioned fear was more reliant on prefrontal regions than was a rat’s ability to freeze in response to an evolutionarily-relevant predator (Canteras, 2003). Even within the same general structure, different subregions may be responsive to ontogenetic versus phylogenetic stimuli; within the mouse olfactory lobe, the glomerular structures that respond to unconditioned odors and lead to an innate fear response are not the same as those that respond to conditioned fear-evoking stimuli (Kobayakawa et al., 2007), and different nuclei of the amygdala have been implicated in innate versus learned fear responses in rats (Thompson, Sullivan, & Wilson, 2008).

These studies suggest that, at least in nonhuman animals, fear responses elicited via phylogenetic means rely on different neural circuitry than those elicited via ontogenetic factors. Although there has not been research directly examining this topic in humans, there have been studies implicating the orbitofrontal cortex (OFC), anterior cingulate cortex (aCC), and other frontal regions with emotional conditioning and associative learning (e.g., Gottfried & Dolan, 2004; Ohman & Mineka, 2001). This hypothesis tested in the present study was that the distinction held both for fear- and pleasure-evoking stimuli. These results suggest that the neural mechanisms supporting emotion processing can differ based on a stimulus’s evolutionary import, with frontal processes recruited when a stimulus’s salience is ontogenetic.

Neural Response to Emotional Stimuli of Phylogenetic and Ontogenetic Significance

Responses to affective stimuli are often discussed within an evolutionary framework, yet not all affective information has evolutionary significance. The present fMRI study compared neural activity to affective stimuli of phylogenetic (e.g., spider, smiling baby) versus ontogenetic (e.g., gun, money) origin. We hypothesized that the orbitofrontal cortex (OFC)—a region required to learn the affective import of information—would be more active when participants processed ontogenetic versus phylogenetic stimuli. The results supported this hypothesis, and the distinction held both for fear- and pleasure-evoking stimuli. These results suggest that the neural mechanisms supporting emotion processing can differ based on a stimulus’s evolutionary import, with frontal processes recruited when a stimulus’s salience is ontogenetic.

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reveal differences in other brain regions as well. We were particularly interested in whether the subcortical regions of the amygdala or the basal ganglia, regions frequently linked to arousal and affective processing (Phan, Wager, Taylor, & Liberzon, 2002; Sergerie, Chochol, & Armony, 2008) would show a differential response for ontogenetic versus phylogenetic stimuli. In our experiment, we reanalyzed data from two prior functional magnetic resonance imaging (fMRI) studies (Kensinger, Garoff-Eaton, & Schacter 2007; Kensinger & Schacter, 2008) to examine how neural response differed when participants viewed fear- or pleasure-evoking stimuli of phylogenetic or ontogenetic origin. Stimuli of ontogenetic origin would be items such as guns, cars, accidents, balloons, or money, because these types of stimuli have an affective connotation that has been learned. By contrast, stimuli of phylogenetic origin would be items such as snakes, fires, lions, babies, or smiling faces, because these items would have evolutionary relevance.

Method

Participants

This experiment reanalyzed data from 29 participants (12 men and 17 women; ages 18-35) from two prior experiments (14 from Kensinger et al., 2007; 15 from Kensinger & Schacter, 2008). All participants were right-handed, native English speakers, and informed consent had been obtained from all participants in a method approved by the Boston College, Harvard University, and Massachusetts General Hospital Institutional Review Boards. Participants were recruited via fliers posted throughout the Boston area, and participants received $25/hour for their participation. All participants were screened to exclude those with a history of neurological trauma or psychiatric disorder. No participant was taking any centrally acting medications.

Materials and Procedure

Materials comprised colored, nameable photo objects (Hemera Technologies, www.hemera.com). We selected images from this dataset if they seemed likely to be classified as positive (e.g., penguin, smiling baby), negative (e.g., snake, grenade), or neutral (e.g., canoe, blender) in valence. Twenty participants, separate from those who participated in the fMRI study but meeting the same eligibility criteria, rated 592 objects that had been selected from the Hemera Technologies database on two dimensions: image valence, referring to how positive or negative an image was, and image arousal, referring to the calming/subduing or exciting/agitating nature of an image, following guidelines outlined by Ito, Cacioppo, and Lang (1998). Participants rated valence and arousal on 9-point Likert-type scales as described in two prior studies (Kensinger et al., 2007; Kensinger & Schacter, 2008). We then separated the rated objects into negative and arousing (valence ratings of less than 3.5 and arousal ratings of greater than 5 on 9-point Likert scales), positive and arousing (valence ratings greater than 5.5 and arousal ratings greater than 5), and neutral and nonarousing (valence ranging between 3 and 6 and arousal less than 5) groups. We excluded images that did not fall into any of these categories.

From these groups, we further classified the objects by evolutionary relevance (ontogenetic or phylogenetic) using our best judgment. “Phylogenetic” picture objects contained features or objects presumed to have been encountered in ancestral environments and thus most likely to elicit unconditioned responses. Such objects included human faces, fangs, stinggers, sharp objects, or gory scenes (low valence and fear-relevant) and lush environments, happy infants, or people in seductive poses (high valence and pleasure-relevant). “Ontogenetic” picture objects contained features or objects characteristic of contemporary society and that could not have been encountered in ancestral environments. Such objects included guns, bombs, or car crashes (low valence and fear-relevant) and celebratory scenes with no people, balloons, or trophies (high valence and pleasure-relevant).

We classified neutral picture objects (medium valence, low arousal) into organic and man-made groups to provide controls for phylogenetic and ontogenetic object groups respectively. We included these neutral object groups in our experiment in order to rule out possible processing differences between organic and man-made objects, such as those due to object complexity differences, as causes for differential activity between phylogenetic and ontogenetic object types. Two hundred and nine out of the total 592 picture objects were successfully classified as fear-phylogenetic, pleasure-phylogenetic, fear-ontogenetic, pleasure-ontogenetic, neutral-organic, or neutral-man-made, and we restricted analyses to these items. If the classification of certain objects proved ambiguous, or if certain objects did not fit neatly in previously mentioned categories, we omitted these objects from the analyses.

Study Procedure

We presented a series of nameable, colored objects for 1 sec each to participants while in the fMRI scanner. Participants made either a size decision about whether each object, in the real world, would fit inside a filing cabinet drawer (in Kensinger & Schacter, 2008) or about whether the object was a living thing (in Kensinger et al., 2007). The goal of having a task was to
assure that the participant was attending to each item, and these particular tasks were chosen because they did not focus the participants on an evaluation of the affective meaning of the objects. Following the item’s presentation, a fixation cross (+) appeared for a variable duration (range of 5–13 sec) to provide different delays between the start of the sampling of brain images and start of stimulus presentations, or “jitter,” required to isolate the hemodynamic response to each event.

**Image Acquisition**

We used a 3.0 Tesla Siemens Allegra MRI scanner to acquire structural images of the brain and to provide information about changes in the blood-flow response to different regions of the brain as participants viewed the photo objects. To gather the structural images of the brain, we used a multiplanar rapidly acquired gradient-echo (MP-RAGE) sequence. To provide the information about the changes in the blood-flow response, we gathered functional images using a T2*-weighted echo-planar imaging (EPI) sequence (TE = 30 msec, FOV = 200 mm; flip angle = 90°). Twenty-eight axial–oblique slices (3.2 mm thickness, 0.6 mm skip between slices), aligned along the anterior commissure/posterior commissure line, were acquired in an interleaved fashion. The parameters were identical in the two studies from which data were analyzed except that in Kensinger et al. (2007) the repetition time (TR) was 2000 msec and in Kensinger and Schacter (2008) it was 3000 msec. This discrepancy has to do with how often “snapshots” of the blood-flow response were taken (i.e., every 2000 msec vs. every 3000 msec), but because the blood-flow response is quite sluggish (blurring over approximately 6 seconds), this discrepancy should not have influenced the results.

**Data Analysis**

We conducted preprocessing and data analysis within Statistical parametric mapping software “SPM2” (Wellcome Department of Cognitive Neurology, www.fil.ion.ucl.ac.uk/spm). The functional data underwent standard preprocessing. This preprocessing takes steps to minimize the noise created by a number of different sources: by participant head motion, by the order in which different “slices” of the brain are imaged, and by variability in the size and shape of participant brains.

We specified six different types of events for each participant based upon previous classifications: fear-phylogenetic, fear-ontogenetic, pleasure-phylogenetic, pleasure-ontogenetic, neutral-phylogenetic, and neutral-ontogenetic. Fear objects had high arousal scores and low valence scores, pleasure objects had high arousal scores and high valence scores, and neutral objects had low arousal scores and medium valence scores. For every participant, and on a voxel-by-voxel basis (a voxel is similar to a pixel, but is in three dimensions rather than two), we conducted an event-related analysis in which all instances of a particular event type were modeled through convolution with a canonical hemodynamic response function. These data were entered into second-level, random-effects group analyses.

We conducted group comparison analyses to reveal regions with at least a 5-voxel extent and a peak voxel significance of $p < .001$. To characterize the patterns of hemodynamic response within regions revealed in the contrast analyses, we created regions of interest (ROIs) that included all significant voxels within a 5-mm sphere (using the ROI toolbox implemented in MarsBar; Brett, Anton, Valabregue, & Poline, 2002). The hemodynamic time course for each individual participant and for each condition type (relative to fixation baseline) was extracted. We performed statistics on the sum of the signal changes occurring between 3 sec and 12 sec poststimulus onset, and these sums appear in the figures.

We presented all activations in neurological coordinates (i.e., activity on the right hemisphere is presented on the right side of the brain images). We reported voxel coordinates in Talairach coordinates (from Talairach & Tournoux, 1988). These coordinates reflect the most significant voxel within a cluster of activation.

**Results**

**Behavioral Results**

We analyzed object ratings to make sure that fear-phylogenetic, fear-ontogenetic, pleasure-phylogenetic, and pleasure-ontogenetic objects had comparable arousal scores to each other and significantly higher arousal scores than neutral-phylogenetic and neutral-ontogenetic objects. We also made sure that fear-phylogenetic and fear-ontogenetic objects had comparably low valence scores, that neutral-phylogenetic and neutral-ontogenetic objects had comparably high arousal scores, and that pleasure-phylogenetic and pleasure-ontogenetic objects had comparable high valence scores (Table 1). To make these comparisons, a repeated-measures ANOVA was conducted for (a) valence ratings and (b) arousal ratings (based on the earlier data gathered from 20 participants who did not participate in the current experiment). Each ANOVA included object type (phylogenetic, ontogenetic) and emotion type (fear, happy, neutral) as factors. In both ANOVAs, there was no main effect of object type, nor an interaction with object type ($p > .15$), revealing that the object type did not influence the valence or arousal.
ratings of the stimuli. A similar repeated-measures ANOVA conducted on the reaction times that it took each participant within the MRI study to respond to each stimulus also revealed no main effects nor interactions; therefore, importantly, the reaction time did not differ between ontogenetic or phylogenetic event subtypes ($p > .15$; Table 1). Thus, differences in the amount of time processing the stimuli should not have confounded our results.

**fMRI Results**

The first analysis used an ANOVA to specifically examine regions that showed an interaction between emotion type (fear, neutral) and evolutionary relevance (ontogenetic, phylogenetic), showing a stronger response for items that were both fear-relevant and of ontogenetic origin. To be considered significant, regions had to consist of at least 5 contiguous voxels with an $F > 3.5$, $p < .001$. This analysis revealed that activity within a region spanning the left aCC and OFC (Talairach coordinates -16, 39, -2) responded more to ontogenetic compared to phylogenetic fear-relevant stimuli. This region did not show a comparable effect for the neutral stimuli, thereby ruling out that this response was a more general response to man-made as opposed to natural objects (see Figure 1). Similar patterns of activity were revealed within regions of the right aCC (Talairach coordinates: 20, 47, -2) and dorsal PFC (Talairach coordinates: 16, 60, 0).

A second analysis examined regions that showed an interaction between emotion type (fear, neutral) and evolutionary relevance (ontogenetic, phylogenetic), because of a stronger response for items that were both fear-relevant and of phylogenetic origin. At the standard threshold typically used in fMRI research for this type of interaction analysis, $F > 3.5$, $p < .001$, no regions showed this pattern of response. At a lowered threshold, $F > 3.0$, $p < .005$, regions of the lingual gyrus (Talairach coordinates: -42, -40, 0) and right dorsal striatum (Talairach coordinates: -16, 6, 8) responded more to phylogenetic compared to ontogenetic pleasure-evoking stimuli, but showed no differential response for man-made versus organic neutral stimuli.

Notably absent from these analyses was activity within the amygdala. To examine whether the amygdala might respond to all affective stimuli regardless of their evolutionary relevance, we conducted a conjunction analysis to reveal the regions that were elicited by fear- and pleasure-evoking stimuli of both ontogenetic and phylogenetic relevance. This conjunction analysis required neural activity to be present in four contrasts: fear-ontogenetic versus neutral, fear-phylogenetic versus neutral, pleasure-ontogenetic versus neutral, pleasure-phylogenetic versus neutral. The $p$ value required for

<table>
<thead>
<tr>
<th>TABLE 1.</th>
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<td>Mean (SE) Valence Ratings, Arousal Ratings, and Reaction Times as a Function of the Valence and Evolutionary Category of Stimuli.</td>
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<table>
<thead>
<tr>
<th></th>
<th>Fear-Evoking</th>
<th>Pleasure-Evoking</th>
<th>Neutral</th>
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<tbody>
<tr>
<td></td>
<td>Ontogenetic</td>
<td>Phylogenetic</td>
<td>Ontogenetic</td>
</tr>
<tr>
<td>Valence</td>
<td>2.31 (.08)</td>
<td>2.25 (.05)</td>
<td>6.61 (.2)</td>
</tr>
<tr>
<td>Arousal</td>
<td>6.76 (.15)</td>
<td>6.68 (.17)</td>
<td>6.71 (.16)</td>
</tr>
<tr>
<td>Reaction time</td>
<td>2.05 (.09)</td>
<td>2.07 (.10)</td>
<td>2.00 (.09)</td>
</tr>
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</table>

The third analysis examined regions that showed an interaction between emotion type (pleasure, neutral) and evolutionary relevance (ontogenetic, phylogenetic), with a stronger response to stimuli that were both pleasurable and also ontogenetic (all regions revealed were significant at values of $F > 3.5$, $p < .001$). As with the fearful stimuli, pleasure-ontogenetic stimuli elicited disproportionate activity in comparison to pleasure-phylogenetic stimuli or to any type of neutral stimulus in a cluster spanning the right OFC/aCC (Talairach coordinates: 32, 42, -6).

A fourth analysis examined regions that showed an interaction between emotion type (pleasure, neutral) and evolutionary relevance (ontogenetic, phylogenetic), with a stronger response to stimuli that were both pleasurable and also phylogenetic (all regions revealed were significant at values of $F > 3.5$, $p < .001$). Also similar to the regions revealed for the analysis of fearful stimuli, activity within the left fusiform gyrus (Talairach coordinates: -42, -40, 0) and the left dorsal striatum (Talairach coordinates: -16, 6, 8) was enhanced for phylogenetic compared to ontogenetic pleasure-evoking stimuli, but showed no differential response for man-made versus organic neutral stimuli.

As with the fearful stimuli, pleasure-ontogenetic stimuli elicited disproportionate activity in comparison to pleasure-phylogenetic stimuli or to any type of neutral stimulus in a cluster spanning the right OFC/aCC (Talairach coordinates: 32, 42, -6).
each individual contrast entered into the conjunction analysis was thresholded at a liberal \( p < .01 \), but this specification yielded a conservative \( p \) value for the four-way conjunction \( (p < .0001) \). This conjunction analysis did reveal activity within the left amygdala (Talairach coordinates: \(-20, 0, -18\)), suggesting that this region responds to all high-arousal affective stimuli regardless of valence or evolutionary relevance.

**Discussion**

The results of this experiment supported our hypothesis that stimuli whose affective relevance was ontogenetic would be processed with more aCC/OFC activity than stimuli whose affective relevance was of phylogenetic origin. This disproportionate frontal-based response to ontogenetic stimuli held for both fear- and pleasure-evoking stimuli, suggesting that the aCC/OFC’s tie to ontogenetic affective stimuli is not valence-specific.

A plethora of studies have implicated these frontal regions in the ability to learn the affective import of information: Individuals with damage to the aCC and OFC have difficulties learning the affective value of stimuli, and healthy individuals show robust aCC and OFC activity as they learn about affective contingencies (e.g., O’Doherty, 2007; Rolls & Grabenhorst, 2008). Our results suggest that these same structures that initially allow individuals to acquire affective knowledge continue to be active when individuals later process those stimuli. Even though an individual may have learned the affective qualities (e.g., that money is pleasurable and guns are threatening) of ontogenetic objects long ago, the brain regions that were likely involved in learning those associations seem to be continually active when processing that information.

This disproportionate involvement of the aCC/OFC in the processing of ontogenetic stimuli may provide greater flexibility in a person’s response to that information. It is well known that the OFC can be important for shaping, and reshaping, affective contingencies (Gottfried & Dolan, 2004). For instance, the OFC has been implicated in top-down regulation of affective responses to emotional faces and aversive odors (Floresco & Ghods-Sharifi, 2007; Haber, Kim, Mailly, & Calzavara, 2006), and both the aCC and OFC have been tied to the regulation of emotion and social behavior (Bachevalier & Loveland, 2006; Rudebeck, Bannerman, & Rushworth, 2008).

If affective neural circuits that correspond to ontogenetic associations are more susceptible to frontal cortical modulation than those circuits that correspond to phylogenetic associations, then this phenomenon may shed light on the efficacy of psychological therapy in distinct contexts. Our findings could explain, for example, why fewer phobias occur toward ontogenetic stimuli whereas the majority of phobias are based on fears for natural, or phylogenetic, contexts or objects (Mühlberger et al., 2006). Ontogenetic associations leading to related phobias may be more easily extinguished because they elicit more orbitofrontal activity (Gottfried & Dolan, 2004). Furthermore, our findings suggest that cognitive behavioral therapy (CBT) could prove most useful for patients with phobias for ontogenetic objects (Mühlberger et al., 2006) because such objects already elicit activity in regions like the orbitofrontal cortex, a region thought to be important in extinguishing conditioned stimulus-conditioned response associations (Gottfried & Dolan, 2004), emotional regulation, and cognitive reappraisal (Bachevalier & Loveland, 2006; Rudebeck et al., 2008). Although patients with phylogenetic phobias, like arachnophobia (fear of spiders) or acrophobia (fear of heights), may show some improvement as a result of CBT or similar.
therapies, perhaps their treatment plan should also include the administration of psychotropic drugs such as benzodiazepines that could mitigate certain aspects of the innate fear response.

In addition to fear-ontogenetic objects, pleasure-ontogenetic objects such as a hundred dollar bill are also likely to elicit more variable and malleable cognitive and affective responses that are a consequence of increased frontal cortical activity at the time and context of learning and processing. Regardless of the implications of the distinction, our results emphasize that the frontal regions tied to affective learning and to the ability to sculpt emotional reactions are disproportionately active during the processing of ontogenetic stimuli.

In contrast to the enhanced frontal activity for ontogenetic stimuli, when stimuli were of phylogenetic origin, activity tended to increase within the dorsal striatum. This subcortical region has been tied to the bottom-up processing of emotionally-salient stimuli; through its rapid afferents with other subcortical regions, including the midbrain and amygdala, this region plays an important role in the ability to respond quickly to affective stimuli (e.g., Bowers et al., 2006; LeDoux, 2000). Thus, in stark contrast to ontogenetic stimuli, whose processing seems to be characterized by enhanced activity within regions tied to top-down, flexible affective responding, processing of phylogenetic stimuli seems to be linked to a more bottom-up system that is less defined by frontal cortical modulation and better suited for a direct, more automatic motor response. The relatively nonplastic nature of phylogenetic affective circuits in the brain may explain why certain behaviors, such as smiling, frowning, laughing, or crying are identical across all cultures and even exhibited by individuals born blind (Prohovnik, Skudlarski, Fullbright, Gore, & Wexler, 2004).

It is interesting to note that although the putamen, a region of the dorsal striatum, was associated with the processing of phylogenetic stimuli of either positive or negative valence, there was a laterality difference. Right putamen activity was stronger for negative phylogenetic stimuli whereas left putamen activity was stronger for positive phylogenetic stimuli. It is sometimes true that right-lateralized activity is stronger for negative stimuli (or withdrawal emotions) whereas left-lateralized activity is stronger for positive stimuli (or approach emotions), but these dissociations are often strongest within prefrontal regions. However, there have also been instances where these distinctions have been revealed within subcortical regions (Davidson, 1992; Murphy, Nimmo-Smith, & Lawrence, 2003). It is possible that processing of phylogenetic stimuli is most likely to occur within the subset of regions that are specialized for processing stimuli of a particular valence; in other words, if right-lateralized regions are specialized for processing negative stimuli, those regions may be more likely to show an enhanced response to negative phylogenetic stimuli.

In contrast to the aCC/OFC and putamen – regions that responded differentially based on the evolutionary import of stimuli – the amygdala responded more consistently to all affective stimuli. This finding is consistent with studies that have implicated the amygdala in broad, arousal-based processing and with a growing body of literature suggesting that amygdala activity is not directly tied to the type of affective experience elicited by a stimulus (e.g., Phan et al., 2002; Sergerie et al., 2008). Instead, the amygdala may serve as a core part of the affective processing network, recruited regardless of stimulus valence or evolutionary origin. Although previous research has supported the tie between amygdala activity and the processing of both positive and negative information (Anderson et al., 2003; Garavan, Pendegrass, Ross, Stein, & Risinger, 2001; Hamann, Ely, Hoffman, & Kilts, 2002), to our knowledge this is the first study to directly tease apart its response to stimuli of phylogenetic and ontogenetic origin. Of course, because the current fMRI methods did not have sufficient spatial resolution to tease apart activity within different nuclei of the amygdala, it remains possible that different nuclei of the amygdala may play a role in different forms of affective processing, as described by LeDoux (2000), and may have activity that is modulated by the evolutionary importance of a stimulus.

Conclusion
To gain insight into the interplay of nature and nurture in the shaping of human emotional responses, we conducted an imaging experiment to determine if and how separate brain regions underlie affective processing of phylogenetic and ontogenetic objects. Our results show that the processing of ontogenetic objects is characterized by frontal cortical regions thought to play roles in cognition and emotional regulation. The processing of phylogenetic objects, on the other hand, is characterized by activity in more ancient subcortical regions. This activity may result from robust “fight or flight” and approach circuits that are less influenced by cognition, proved crucial for the survival and reproduction of ancestral people, and are somehow represented in the human genome. The frontal cortical activity elicited by ontogenetic object processing may support more malleable and variable stimulus-response associations for objects that are emotionally ambiguous from an evolutionary perspective.
References


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