FEATURE ARTICLE
Famous Faces Activate Contextual Associations in the Parahippocampal Cortex

Moshe Bar[1], Elissa Aminoff[1] and Alumit Ishai[2]

[1]Martinos Center at Massachusetts General Hospital, Harvard Medical School, Charlestown, MA 02129, USA and [2]Institute of Neuroradiology, University of Zurich, 8057, Switzerland

The parahippocampal cortex (PHC) has been traditionally implicated both in place processing and in episodic memory. How could the same cortical region mediate these cognitive functions that seem quite different? We have recently proposed that the PHC should be seen as more generally mediating contextual associative processing, which is required for both navigation and memory. We therefore predicted that any associative objects should activate the PHC. To test this generalization, we investigated the extent to which common stimuli that are nonspatial by nature, namely faces, activate the PHC, although their perception is typically associated with other cortical structures. Specifically, we compared the activation elicited by famous faces, which are highly associated with rich pictorial and contextual information (e.g., Tom Cruise) and are not associated with a specific place, with activation elicited by unfamiliar faces. Consistent with our prediction, contrasting famous with unfamiliar faces revealed significant activation within the PHC. Taken collectively, these findings indicate that the PHC should be regarded as mediating contextual associations in general and not necessarily spatial or episodic information.

Keywords: associations, context, face processing, parahippocampal cortex

Introduction

The parahippocampal cortex (PHC) in the medial temporal lobe has been involved in the representation and processing of spatial, place-related information (Aguirre et al. 1996; Maguire et al. 1997; Epstein and Kanwisher 1998; Bohbot et al. 2000; Mellet et al. 2000; Levy et al. 2001), and a significant subregion within the PHC has been termed "parahippocampal place area" (PPA) (Epstein and Kanwisher 1998). In the community that studies memory, however, the PHC has been widely known to subserve episodic memory (Gabrieli et al. 1997; Brewer et al. 1998; Wagner et al. 1998; Schacter and Wagner 1999; Davachi et al. 2003; Ranganath et al. 2004; Squire et al. 2004). Therefore, it has previously been unclear how could the same region mediate seemingly different cognitive functions (Fig. 1).

Although spatial processing functions are generally different from episodic memory, they rely on similar elements. We have recently proposed that these shared elements are provided by contextual associations (Bar and Aminoff 2003; Bar 2004; Aminoff et al. 2007) and showed that the PHC is differentially activated for a wide range of familiar and newly learned contextual associations (Fig. 2).

In our initial experiments (Bar and Aminoff 2003), we compared the functional magnetic resonance imaging (fMRI) activation elicited when participants viewed pictures of individual objects that are highly associated with a certain context (e.g., a cowboy hat) with the activation elicited by individual objects that were not strongly associated with any context (e.g., a camera). Contextual associations differentially activated a network including the PHC, retrosplenial complex, and parts of the medial prefrontal cortex (Fig. 2A). Activation within this network has since been found to be robust and highly replicable (Bar and Aminoff 2003; Bar 2004; Aminoff et al. 2007; Diana et al. forthcoming). Standardized localizer information can be found at http://barlab.mgh.harvard.edu/ContextLocalizer.htm.

Given that the PHC activation elicited by strongly contextual objects seemed to overlap with the activation reported in the PPA (Epstein and Kanwisher 1998; Epstein et al. 1999), it was unclear whether our activation was mainly due to contextual associations or the result of an indirect activation of specific places, which in turn activated the PPA. We therefore conducted a second study where the highly contextual objects were clearly separated for spatial contextual objects (e.g., a construction hat) and highly contextual objects that are associated with nonspatial contexts (e.g., cupid). Both conditions activated the same contextual network (Fig. 2B). Interestingly, we found segregation in the PHC between the activation elicited by spatial and nonspatial contexts, whereby spatial contexts activate primarily the posterior part of the PHC and the nonspatial contexts activate a more anterior, adjacent part of the PHC (Bar and Aminoff 2003).

In a third study (Aminoff et al. 2007), we created novel objects and relations, such that participants did not have any subjective associations and memories with the new stimuli beyond those on which they were trained prior to scanning. The findings of this experiment (see Fig. 2c) corroborated our previous findings and thus added support to our proposal that the PHC is involved in both spatial and nonspatial contextual associations.

Associations are required to link landmarks to places in spatial processes, and contextual associations are needed to glue the constituents of an episode in memory. Consequently, by modifying the ascription of a role to the PHC to be mediating contextual associative representations and processing in general, findings from various experiments can be naturally reconciled. A critical test of our hypothesis is whether complex stimuli with contextual but not spatial associations would also activate the PHC. Therefore, we compared here PHC activation elicited by famous faces, which evoke a large amount of contextual associations that are not particularly spatial, with the PHC activation elicited by unfamiliar faces.

Face perception is a highly developed visual skill in humans, which is mediated by activation in a distributed neural system that encompasses visual, limbic, and prefrontal regions (Ishai
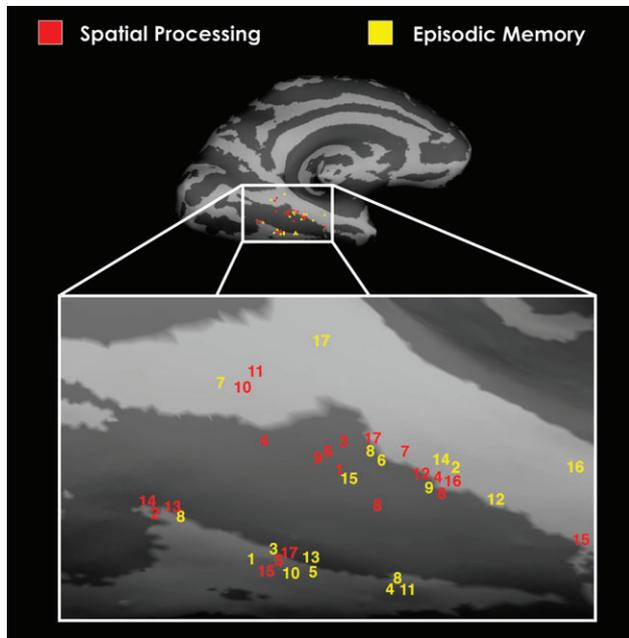
Figure 1. Spatial and episodic processing in the PHC. A comparison of Talairach coordinates from the spatial processing literature (17 studies) and the episodic memory literature (17 studies). Spatial processing (numbers marked in red): (1) Epstein et al. (1999), (2) Epstein et al. (2003), (3) Levy et al. (2001), (4) Goh et al. (2004), (5) Gorno-Tempini and Price (2001), (6) O'Craven and Kanwisher (2000), (7) Janzen and van Turennout (2004), (8) Mellet et al. (2000), (9) Maguire et al. (1997), (10) Rosenbaum et al. (2004), (11) Shelton and Gabrieli (2002), (12) Sugiura et al. (2005), (13) Yi and Chun (2005), (14) Steeves et al. (2004), (15) Goel et al. (2004), (16) Suzuki et al. (2005), and (17) Burgess et al. (2001). Episodic memory (numbers marked in yellow): (1) Wagner et al. (1998), (2) Medford et al. (2005), (3) Sommer et al. (2005), (4) Morcom et al. (2003), (5) Davachi et al. (2003), (6) Kirchhoff et al. (2000), (7) Casasanto et al. (2002); (8) Brewer et al. (1998), (9) Reber et al. (2002), (10) Takahashi et al. (2002), (11) Dobbins et al. (2003), (12) Henke et al. (1999), (13) Yonelinas et al. (2001), (14) Pihlajamaki et al. (2003); Kirwan and Stark (2004), (16) Tsukiura et al. (2002), and (17) Ranganath et al. (2003). Reproduced with permission from Aminoff et al. (2007).

et al. 2005; Fairhall and Ishai 2007). Specifically, the cortical network that mediates face perception includes the fusiform gyrus, an extrastriate region that processes the identification of individuals (Kanwisher et al. 1997; Ishai et al. 1999; Grill-Spector et al. 2004); the superior temporal sulcus (Hoffman and Haxby 2000; Puce et al. 2003); the amygdala and insula (Breiter et al. 1996; Ishai et al. 2004); the inferior frontal gyrus, where semantic aspects are processed (Leveroni et al. 2000; Ishai et al. 2002); and regions of the reward circuitry, including the nucleus accumbens and orbitofrontal cortex (Aharon et al. 2001; O'Doherty et al. 2003; Kranz and Ishai 2006; Ishai 2007). In most previous studies, the response to faces was contrasted with assorted common objects to localize the fusiform face area (FFA) (e.g., Kanwisher et al. 1997) or with scrambled faces to localize the underlying network (e.g., Ishai et al. 2002; Ishai et al. 2004).

Familiar (e.g., famous) faces elicit enhanced activation in various face-responsive regions (Ishai et al. 2005). In addition, however, famous faces are associated with rich amount of contextual and pictorial information, without being associated with particular spatial information (e.g., Angelina Jolie's face elicits associations about her appearance in *Mr. and Mrs. Smith*, her liaison with Brad Pitt, her adopted children, and her humanitarian work in Africa). Therefore, famous faces are optimal for testing our critical generalization and for contrast-
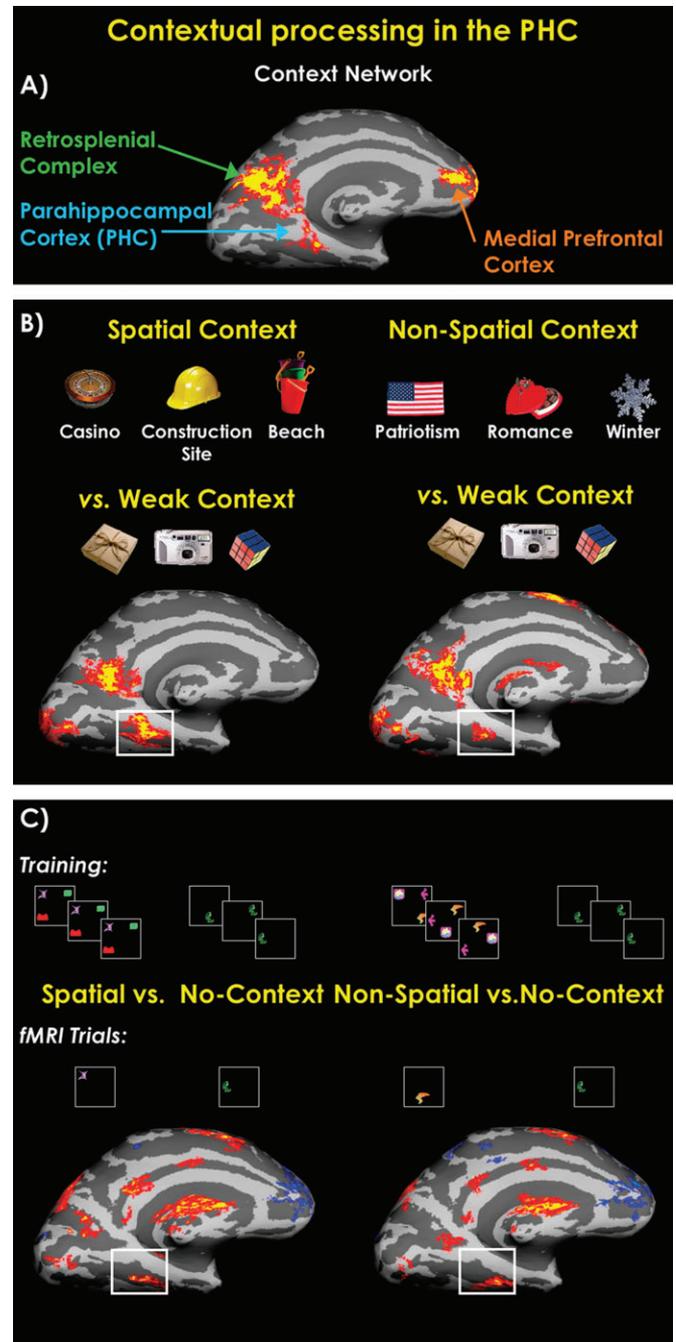

Figure 2. Summary of our previous studies of contextual associations. (*A*) Medial activation for the contrast between strong contextually associative objects and weakly contextual objects. This statistical map was derived from averaging together this strong versus weak contrast from 6 different experiments, of which various tasks were used, with a total of 68 participants (Bar et al. 2007). (*B*) A demonstration that both objects strongly related to specific spatial context, or a place, and objects strongly related to a nonspatial context (e.g., romance) significantly activate the PHC when compared with weak contextual objects (Bar and Aminoff 2003). (*C*) A further demonstration that the PHC processes contextual associations. Participants were trained to learn both spatial and nonspatial associations between novel shapes. At test, participants were scanned when only viewing 1 shape at a time. Statistical maps show the comparison of viewing shapes associated with a spatial (left) or a nonspatial (right) context compared with no-context shapes (Aminoff et al. 2007).

ing the 2 hypotheses: If the PHC contains a place-specific module (PPA), then it should not be particularly responsive to faces that have no pronounced spatial associations. However, if, as we propose, the PHC more generally mediates contextual

associations, it would exhibit differential activation for famous compared with unfamiliar faces because of the contextual associations they evoke.

Before we proceed, it might be worth elaborating on what we mean by "contextual associations." Our working definition is that items are contextually associated with each other if they typically coappear in the environment around us or their corresponding representations tend to be coactivated. Therefore, a desk and a chair are contextually associated because they tend to appear together, but a cupid and a heart-shaped chocolate box are also contextually associated with each other, even if they do not typically physically appear next to each other. Furthermore, the strength of the associations, rather than their number, is the primary dimension that determines whether a certain visual stimulus is considered strongly or weakly contextually associative. For example, a flyswatter is associated only with a fly. A refrigerator, on the other hand, is associated with many objects that tend to share its context. Both a flyswatter and a refrigerator are considered strongly contextual objects, which is also reflected in the consensus observed in participants' responses (Bar and Aminoff 2003). Objects that we consider weakly contextual objects (e.g., a camera or a bottle of water), on the other hand, are associated with many objects, but only weakly, and most importantly, these associates do not share the same context. There are many such strong associations for the famous faces, whereas they are nonexistent for the unfamiliar faces in our critical comparisons.

Materials and Methods

The methods described here pertain exclusively to the face study, which is also the study for which we present new results here. For detailed descriptions of the material and methods used in the studies of contextual processing with objects and shapes, see Bar and Aminoff (2003); Aminoff et al. (2007); and Bar et al. (2007).

Participants
Ten healthy participants (5 males, mean age 25 years) with normal vision participated in the study. All participants gave written informed consent in accordance with protocols approved by the University Hospital of Zurich.

Stimuli and Tasks
Participants were presented with grayscale photographs of unfamiliar neutral and emotional (fearful and happy) faces and neutral famous faces. The famous faces consisted of contemporary Hollywood celebrities, taken from the database of Ishai et al. (2002). Phase-scrambled versions of these faces were used as visual baseline (Ishai et al. 2005). Each stimulus was presented for 3 s. Each run included 3 alternating epochs of scrambled faces (24 s) and faces (36 s). Four runs were collected per each participant, and the order of stimulus formats was randomized. In each block, 12 faces were presented, namely 36 faces per run and a total of 144 faces in the experiment. Stimuli were generated using Presentation (http://www.neurobs.com, version 9.13) and were projected with a magnetically shielded LCD video projector onto a translucent screen. The subject was instructed to view the faces attentively.

Data Acquisition
Data were collected using a 3T Philips Intera whole-body MR scanner. Functional data were obtained from 39 transverse slices covering the whole brain with a spatial resolution of 2.3 × 2.3 × 3 mm (acquisition matrix 96 × 96), using a sensitivity-encoded single-shot gradient-echo planar sequence. Images were acquired with field of view = 220 mm, time repetition [TR] = 3000 ms, time echo [TE] = 35 ms, $\theta = 82°$ and with a SENSE acceleration factor of 2.0 (Pruessmann et al. 1999). High-resolution spoiled gradient recalled echo structural images were obtained with 1 × 1 × 1-mm spatial resolution (acquisition matrix 224 × 224), TE = 2.30 ms, TR = 20 ms, $\theta = 20°$. These T_1-weighted images provided detailed anatomical information for the region of interest analysis.

Data Analysis
Data were analyzed using SPM5 software (http://www.fil.ion.ucl.ac.uk/spm/). All volumes were slice time corrected, realigned to the first volume, corrected for motion artifacts, mean adjusted by proportional scaling, normalized into standard stereotactic space (template provided by the Montreal Neurological Institute [MNI]), and smoothed using a 5-mm full-width-at-half-maximum Gaussian kernel. The time series were high-pass filtered to eliminate low-frequency components (filter width 128 s) and adjusted for systematic differences across trials. The statistical analysis was based on a conventional general linear model (Friston, Holmes, Poline, et al. 1995; Friston, Holmes, Worsley, et al. 1995). To test our hypothesis, famous faces were contrasted with unfamiliar faces (for the main effect analysis see Ishai et al. 2005). Montreal Neurological Institute coordinates were converted to the normalized space of the brain atlas (Talairach and Tournoux 1988).

Results

We report here novel findings showing that famous faces also activate the PHC. The data from object studies with which these results overlap have been published previously and are overviewed in the Introduction.

When contrasted with scrambled faces, face stimuli elicit significant activation within multiple visual, limbic, and prefrontal regions (Fig. 3). To contrast our contextual association hypothesis with the PPA hypothesis, we reanalyzed the data set of Ishai et al. (2005) and directly compared famous faces with unfamiliar faces. Critically, the PHC region (mean Talairach coordinates: $x = -20$, $y = -36$, $z = -10$) responded significantly more strongly to famous than unfamiliar faces ($P < 0.001$) (Fig. 4). All face stimuli were equated for size and other low-level features, and indeed, given that the faces in the 2 conditions did not significantly differ in any dimension other than the information associated with the famous faces, we did not observe significant activation in any other face-responsive region. Additionally, in the postscan debriefing, all participants reported that when they viewed the famous faces, they spontaneously remembered other pictures of these celebrities and information they knew about them from the tabloids and their recent movies. In contrast, viewing unfamiliar faces did not elicit any associations or recall of prior knowledge about these faces. In summary, when compared with unfamiliar faces, for which no prior knowledge exists, viewing famous celebrities evokes rich contextual associations that resulted in the PHC activation.

To demonstrate the generalization we are proposing here, Figure 4 shows a comparison of old and new contrasts involving different stimuli, tasks, and conditions: the statistical maps and differential activation evoked by scenes, objects, and faces. Across all 4 contrasts, it is clear that stimuli with rich contextual associations activate the PHC significantly, regardless of whether these associations are related to places or not. Overall, this remarkable compatibility between the activations elicited by various objects and famous faces provides significant support to our proposal that the PHC mediates contextual associations in general, rather than spatial associations proper.
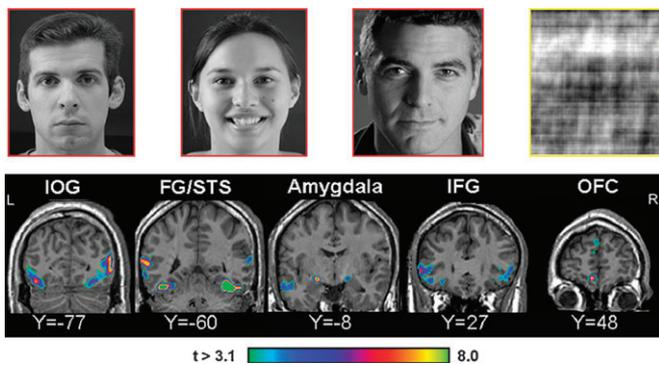
Figure 3. When various face stimuli (e.g., unfamiliar and famous faces) are contrasted with scrambled faces, activation is found within a distributed cortical network that includes visual, limbic, and prefrontal regions. Coronal sections, taken from a representative subject, illustrate activation within the inferior occipital gyrus (IOG); fusiform gyrus (FG), superior temporal sulcus (STS); amygdala; inferior frontal gyrus (IFG); and orbitofrontal cortex (OFC). Coordinates are in the Talairach space. Adapted from Ishai et al. (2005).

Discussion

To reconcile the various cognitive functions that elicit activation in the PHC, we have proposed that this region should be considered as mediating contextual associations in general, without committing to a specific type of associations (Bar and Aminoff 2003; Aminoff et al. 2007; Bar et al. forthcoming). The new findings reported here, that famous faces activate the PHC, support a critical prediction that was derived from this proposal and provide complementary evidence that allows a generalization of this proposal. Specifically, we found that when faces are highly associative, they activate areas involved in contextual associations in the PHC, although faces, when compared with assorted common objects, evoke activation predominantly in the FFA (Kanwisher et al. 1997; Gorno-Tempini and Price 2001; Grill-Spector et al. 2004). There have been some reports showing that famous faces activate the PHC (Sergent et al. 1992; Leveroni et al. 2000; Trauner et al. 2004; Pourtois et al. 2005). Although these previous reports did not make a reference to context and associations, they support our findings and overarching proposal.

Faces that are personally familiar differ from famous faces in terms of emotional attachment and intimate knowledge about biographical information. When personally familiar faces are compared with famous faces, stronger activation is observed in the fusiform gyrus, posterior superior temporal sulcus, posterior cingulate/precuneus, and the paracingulate cortex (Gobbini et al. 2004). Activation in these regions, previously associated with theory of mind (Gallagher and Frith 2003) and the brain's "default" network, suggests that viewing personally familiar faces elicits spontaneous retrieval of social and personal knowledge associated with close friends and family members. This is in accordance with our previous observation of a major overlap between the cortical network mediating contextual associations and the default network (Bar et al. 2007). Taken collectively, these findings suggest that the response to faces is modulated not only by the degree of visual familiarity but importantly by the concomitant associations involved.

It is of interest that although most of the famous faces used in our study were also attractive faces, the comparison with the unfamiliar faces did not reveal enhanced activation in the orbitofrontal cortex. Our previous studies have shown that
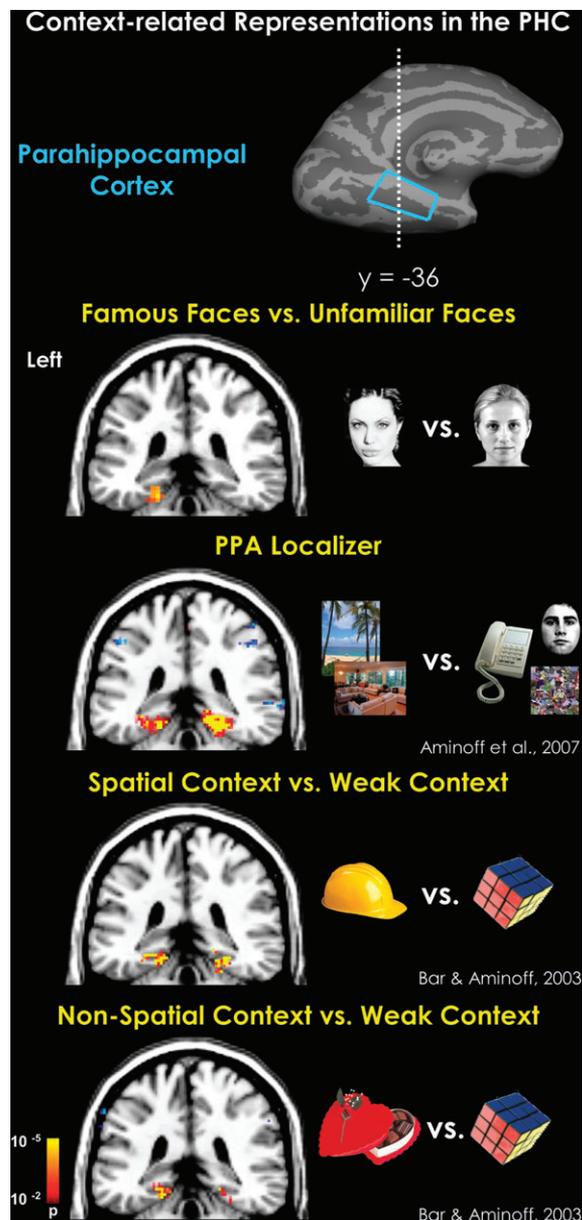

Figure 4. PHC activations by places, spatial context, nonspatial context, and famous faces. Across all contrasts, highly associative stimuli differentially and significantly activated the PHC, regardless of nature of the stimulus and the type of associations (Bar and Aminoff 2003; Aminoff et al. 2007).

attractive faces evoke stronger activation in the orbitofrontal cortex (Kranz and Ishai 2006; Ishai 2007). Therefore, our current findings suggest that beauty was implicit to the spontaneous retrieval of contextual associations associated with these famous faces.

We did not observe stronger activation to famous than unfamiliar faces in other regions of the contextual processing network, namely the retrosplenial complex and the medial prefrontal cortex. This lack of activation could be explained in terms of cognitive demands. Tasks that involve recognition, generation of mental images, and retrieval from episodic memory are more likely to evoke activation within these regions than passive viewing (Ishai et al. 2000; Ishai et al. 2002; Bar and Aminoff 2003; Yago and Ishai 2006; Aminoff et al. 2007; Bar et al. 2007; Aminoff et al., forthcoming).

Finally, our current findings revealed an intriguing hemispheric asymmetry. As can be seen in Figure 4, nonspatial information seems to elicit stronger activation in the left hemisphere, whereas spatial information seems to elicit stronger activation in the right hemisphere. Although face stimuli evoke stronger activation in the right hemisphere (Ishai et al. 2005), contrasting famous faces with unfamiliar ones resulted in a significant cluster in the left PHC. These findings are consistent with prior studies of visual imagery of faces, in which stronger activation was found in the left hemisphere (Ishai et al. 2000; Ishai et al. 2002). Given that imagery and contextual activation share the property of activating representations of information that is not physically present, this convergence supports our proposal that viewing famous faces elicits contextual associations, possibly mediated by semantic knowledge stored in the left hemisphere. Future studies will determine the extent to which this hemispheric asymmetry can be generalized.

In summary, using faces, we have extended our previous studies (Bar and Aminoff 2003; Bar 2004; Aminoff et al. 2007; Bar et al. 2007) and provided additional strong support to our proposal that the operation of the PHC, including the PPA within it, is best explained as mediating contextual associations.

Funding

Notes

References

Aguirre GK, Detre JA, Alsop DC, D'Esposito M. 1996. The parahippocampus subserves topographical learning in man. Cereb Cortex. 6:823-829.

Aharon I, Etcoff N, Ariely D, Chabris CF, O'Connor E, Breiter HC. 2001. Beautiful faces have variable reward value: fMRI and behavioral evidence. Neuron. 32:537-551.

Aminoff E, Gronau N, Bar M. 2007. The parahippocampal cortex mediates spatial and non-spatial associations. Cereb Cortex. 27:1493-1503.

Aminoff E, Schacter DL, Bar M. Forthcoming. The cortical underpinnings of context-based memory distortion.

Bar M. 2004. Visual objects in context. Nat Rev Neurosci. 5:617-629.

Bar M, Aminoff E. 2003. Cortical analysis of visual context. Neuron. 38:347-358.

Bar M, Aminoff E, Mason M, Fenske M. 2007. The units of thought. Hippocampus. 17:420-428.

Bar M, Aminoff E, Schacter DL. Forthcoming. Scenes unseen: the parahippocampal cortex subserves contextual associations, not scenes per se.

Bohbot VD, Allen JJ, Nadel L. 2000. Memory deficits characterized by patterns of lesions to the hippocampus and parahippocampal cortex. Ann N Y Acad Sci. 911:355-368.

Breiter HC, Etcoff NL, Whalen PJ, Kennedy WA, Rauch SL, Buckner RL, Strauss MM, Hyman SE, Rosen BR. 1996. Response and habituation of the human amygdala during visual processing of facial expression. Neuron. 17:875-887.

Brewer JB, Zhao Z, Desmond JE, Glover GH, Gabrieli JD. 1998. Making memories: brain activity that predicts how well visual experience will be remembered. Science. 281:1185-1187.

Burgess N, Maguire EA, Spiers HJ, O'Keefe J. 2001. A temporoparietal and prefrontal network for retrieving the spatial context of lifelike events. Neuroimage. 14:439-453.

Casasanto DJ, Killgore WD, Maldjian JA, Glosser G, Alsop DC, Cooke AM, Grossman M, Detre JA. 2002. Neural correlates of successful and unsuccessful verbal memory encoding. Brain Lang. 80:287-295.

Diana RA, Yonelinas AP, Ranganath C. Forthcoming. High-resolution multi-voxel pattern analysis of category selectivity in parahippocampal cortex.

Davachi L, Mitchell J, Wagner A. 2003. Multiple routes to memory: distinct medial temporal lobe processes build item and source memories. Proc Natl Acad Sci USA. 100:2157-2162.

Dobbins IG, Rice HJ, Wagner AD, Schacter DL. 2003. Memory orientation and success: separable neurocognitive components underlying episodic recognition. Neuropsychologia. 41:318-333.

Epstein R, Graham KS, Downing PE. 2003. Viewpoint-specific scene representations in human parahippocampal cortex. Neuron. 37:865-876.

Epstein R, Harris A, Stanley D, Kanwisher N. 1999. The parahippocampal place area: recognition, navigation, or encoding? Neuron. 23:115-125.

Epstein R, Kanwisher N. 1998. A cortical representation of the local visual environment. Nature. 392:598-601.

Fairhall SL, Ishai A. 2007. Effective connectivity within the distributed cortical network for face perception. Cereb Cortex. 17:2400-2406.

Friston KJ, Holmes AP, Poline JB, Grasby PJ, Williams SC, Frackowiak RS, Turner R. 1995. Analysis of fMRI time-series revisited. Neuroimage. 2:45-53.

Friston KJ, Holmes AP, Worsley KJ, Poline JB, Frith CD, Frackowiak RS. 1995. Statistical parametric maps in functional imaging: a general linear approach. Hum Brain Mapp. 2:189-210.

Gabrieli JD, Brewer JB, Desmond JE, Glover GH. 1997. Separate neural bases of two fundamental memory processes in the human medial temporal lobe. Science. 276:264-266.

Gallagher HL, Frith CD. 2003. Functional imaging of "theory of mind". Trends Cogn Sci. 7:77-83.

Gobbini MI, Leibenluft E, Santiago N, Haxby JV. 2004. Social and emotional attachment in the neural representation of faces.[erratum appears in Neuroimage. 2006;32:1484]. Neuroimage. 22:1628-1635.

Goel V, Makale M, Grafman J. 2004. The hippocampal system mediates logical reasoning about familiar spatial environments. J Cogn Neurosci. 16:654-664.

Goh JO, Siong SC, Park D, Gutchess A, Hebrank A, Chee MW. 2004. Cortical areas involved in object, background, and object-background processing revealed with functional magnetic resonance adaptation. J Neurosci. 24:10223-10228.

Gorno-Tempini ML, Price CJ. 2001. Identification of famous faces and buildings: a functional neuroimaging study of semantically unique items. Brain. 124:2087-2097.

Grill-Spector K, Knouf N, Kanwisher N. 2004. The fusiform face area subserves face perception, not generic within-category identification. Nat Neurosci. 7:555-562.

Henke K, Weber B, Kneifel S, Wieser HG, Buck A. 1999. Human hippocampus associates information in memory. Proc Natl Acad Sci USA. 96:5884-5889.

Hoffman EA, Haxby JV. 2000. Distinct representations of eye gaze and identity in the distributed human neural system for face perception. Nat Neurosci. 3:80-84.

Ishai A. 2007. Sex, beauty and the orbitofrontal cortex. Int J Psychophysiol. 63:181-185.

Ishai A, Haxby JV, Ungerleider LG. 2002. Visual imagery of famous faces: effects of memory and attention revealed by fMRI. Neuroimage. 17:1729-1741.

Ishai A, Pessoa L, Bikle PC, Ungerleider LG. 2004. Repetition suppression of faces is modulated by emotion. Proc Natl Acad Sci USA. 101:9827-9832.

Ishai A, Schmidt CF, Boesiger P. 2005. Face perception is mediated by a distributed cortical network. Brain Res Bull. 67:87-93.

Ishai A, Ungerleider LG, Haxby JV. 2000. Distributed neural systems for the generation of visual images. Neuron. 28:979-990.

Ishai A, Ungerleider LG, Martin A, Schouten JL, Haxby JV. 1999. Distributed representation of objects in the human ventral visual pathway. Proc Natl Acad Sci USA. 96:9379-9384.

Janzen G, van Turennout M. 2004. Selective neural representation of objects relevant for navigation. Nat Neurosci. 7:673-677.

Kanwisher N, McDermott J, Chun MM. 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. J Neurosci. 17:4302-4311.

Kirchhoff BA, Wagner AD, Maril A, Stern CE. 2000. Prefrontal-temporal circuitry for episodic encoding and subsequent memory. J Neurosci. 20:6173-6180.

Kirwan CB, Stark CE. 2004. Medial temporal lobe activation during encoding and retrieval of novel face-name pairs. Hippocampus. 14:919-930.

Kranz F, Ishai A. 2006. Face perception is modulated by sexual preference. Curr Biol. 16:63-68.

Leveroni CL, Seidenberg M, Mayer AR, Mead LA, Binder JR, Rao SM. 2000. Neural systems underlying the recognition of familiar and newly learned faces. J Neurosci. 20:878-886.

Levy I, Hasson U, Avidan G, Hendler T, Malach R. 2001. Center-periphery organization of human object areas. Nat Neurosci. 4:533-539.

Maguire EA, Frackowiak RS, Frith CD. 1997. Recalling routes around London: activation of the right hippocampus in taxi drivers. J Neurosci. 17:7103-7110.

Medford N, Phillips ML, Brierley B, Brammer M, Bullmore ET, David AS. 2005. Emotional memory: separating content and context. Psychiatr Res. 138:247-258.

Mellet E, Briscogne S, Tzourio-Mazoyer N, Ghaem O, Petit L, Zago L, Etard O, Berthoz A, Mazoyer B, Denis M. 2000. Neural correlates of topographic mental exploration: the impact of route versus survey perspective learning. Neuroimage. 12:588-600.

Morcom AM, Good CD, Frackowiak RS, Rugg MD. 2003. Age effects on the neural correlates of successful memory encoding. Brain. 126:213-229.

O'Craven KM, Kanwisher N. 2000. Mental imagery of faces and places activates corresponding stimulus-specific brain regions. J Cogn Neurosci. 12:1013-1023.

O'Doherty J, Winston J, Critchley H, Perrett D, Burt DM, Dolan RJ. 2003. Beauty in a smile: the role of medial orbitofrontal cortex in facial attractiveness. Neuropsychologia. 41:147-155.

Pihlajamaki M, Tanila H, Hanninen T, Kononen M, Mikkonen M, Jalkanen V, Partanen K, Aronen HJ, Soininen H. 2003. Encoding of novel picture pairs activates the perirhinal cortex: an fMRI study. Hippocampus. 13:67-80.

Pourtois G, Schwartz S, Seghier ML, Lazeyras F, Vuilleumier P. 2005. View-independent coding of face identity in frontal and temporal cortices is modulated by familiarity: an event-related fMRI study. Neuroimage. 24:1214-1224.

Pruessmann KP, Weiger M, Scheidegger MB, Boesiger P. 1999. SENSE: sensitivity encoding for fast MRI. Magn Reson Med. 42:952-962.

Puce A, Syngeniotis A, Thompson JC, Abbott DF, Wheaton KJ, Castiello U. 2003. The human temporal lobe integrates facial form and motion: evidence from fMRI and ERP studies. Neuroimage. 19:861-869.

Ranganath C, Johnson MK, D'Esposito M. 2003. Prefrontal activity associated with working memory and episodic long-term memory. Neuropsychologia. 41:378-389.

Ranganath C, Yonelinas AP, Cohen MX, Dy CJ, Tom SM, D'Esposito M. 2004. Dissociable correlates of recollection and familiarity within the medial temporal lobes. Neuropsychologia. 42:2-13.

Reber PJ, Wong EC, Buxton RB. 2002. Encoding activity in the medial temporal lobe examined with anatomically constrained fMRI analysis. Hippocampus. 12:363-376.

Rosenbaum RS, Ziegler M, Winocur G, Grady CL, Moscovitch M. 2004. "I have often walked down this street before": fMRI studies on the hippocampus and other structures during mental navigation of an old environment. Hippocampus. 14:826-835.

Schacter DL, Wagner AD. 1999. Medial temporal lobe activations in fMRI and PET studies of episodic encoding and retrieval. Hippocampus. 9:7-24.

Sergent J, Ohta S, MacDonald B. 1992. Functional neuroanatomy of face and object processing. A positron emission tomography study. Brain. 115:15-36.

Shelton AL, Gabrieli JD. 2002. Neural correlates of encoding space from route and survey perspectives. J Neurosci. 22:2711-2717.

Sommer T, Rose M, Weiller C, Buchel C. 2005. Contributions of occipital, parietal and parahippocampal cortex to encoding of object-location associations. Neuropsychologia. 43:732-743.

Squire LR, Stark CE, Clark RE. 2004. The medial temporal lobe. Annu Rev Neurosci. 27:279-306.

Steeves JK, Humphrey GK, Culham JC, Menon RS, Milner AD, Goodale MA. 2004. Behavioral and neuroimaging evidence for a contribution of color and texture information to scene classification in a patient with visual form agnosia. J Cogn Neurosci. 16:955-965.

Sugiura M, Shah NJ, Zilles K, Fink GR. 2005. Cortical representations of personally familiar objects and places: functional organization of the human posterior cingulate cortex. J Cogn Neurosci. 17:183-198.

Suzuki M, Tsukiura T, Matsue Y, Yamadori A, Fujii T. 2005. Dissociable brain activations during the retrieval of different kinds of spatial context memory. Neuroimage. 25:993-1001.

Takahashi E, Ohki K, Miyashita Y. 2002. The role of the parahippocampal gyrus in source memory for external and internal events. Neuroreport. 13:1951-1956.

Talairach J, Tournoux P. 1988. Co-planar stereotaxic atlas of the human brain. New York: Thieme Medical Publishing.

Trauner P, Dieti T, Staedtgen M, Mecklinger A, Grunwald T, Elger CE, Kurthen M. 2004. Recognition of famous faces in the medial temporal lobe. Neurology. 63:1203-1208.

Tsukiura T, Fujii T, Takahashi T, Xiao R, Sugiura M, Okuda J, Iijima T, Yamadori A. 2002. Medial temporal lobe activation during context-dependent relational processes in episodic retrieval: an fMRI study. functional magnetic resonance imaging. Hum Brain Mapp. 17:203-213.

Wagner AD, Schacter DL, Rotte M, Koutstaal W, Maril A, Dale AM, Rosen BR, Buckner RL. 1998. Building memories: remembering and forgetting of verbal experiences as predicted by brain activity. Science. 281:1188-1191.

Yago E, Ishai A. 2006. Recognition memory is modulated by visual similarity. Neuroimage. 31:807-817.

Yi DJ, Chun MM. 2005. Attentional modulation of learning-related repetition attenuation effects in human parahippocampal cortex. J Neurosci. 25:3593-3600.

Yonelinas AP, Hopfinger JB, Buonocore MH, Kroll NE, Baynes K. 2001. Hippocampal, parahippocampal and occipital-temporal contributions to associative and item recognition memory: an fMRI study. NeuroReport. 12:359-363.