

Neural correlates of object indeterminacy in art compositions

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Received 29 March 2007

Available online 21 August 2007

Abstract

Indeterminate art invokes a perceptual dilemma in which apparently detailed and vivid images resist identification. We used event-related fMRI to study visual perception of representational, indeterminate and abstract paintings. We hypothesized increased activation along a gradient of posterior-to-anterior ventral visual areas with increased object resolution, and postulated that object resolution would be associated with visual imagery. Behaviorally, subjects were faster to recognize familiar objects in representational than in both indeterminate and abstract paintings. We found activation within a distributed cortical network that includes visual, parietal, limbic and prefrontal regions. Representational paintings, which depict scenes cluttered with familiar objects, evoked stronger activation than indeterminate and abstract paintings in higher-tier visual areas. Perception of scrambled paintings was associated with imagery-related activation in the precuneus and prefrontal cortex. Finally, representational paintings evoked stronger activation than indeterminate paintings in the temporoparietal junction. Our results suggest that perception of familiar content in art works is mediated by object recognition, memory recall and mental imagery, cognitive processes that evoke activation within a distributed cortical network.

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Keywords: Functional MRI; Imagery; Memory; Paintings; Perception; Recognition

1. Introduction

Visual indeterminacy occurs when subjects view apparently detailed and vivid images that resist object recognition. Indeterminate art compositions invoke an unusual state of awareness in which the formal aspects of perception (color, form and motion) become dissociated from the semantic aspects (association, meaning and memory). In contrast with the habitual mode of seeing, in which visual sensation is accompanied by immediate recognition, the indeterminacy effect presents viewers with an apparently meaningful yet persistently meaningless scene, which they struggle to resolve. Robert Pepperell's paintings and drawings were designed to induce a disrupted perceptual condition: instead of a recognizable depiction, the viewer is presented with a 'potential image' (Gamboni, 2002), that is, a complex multiplicity of possible images, none of which ever finally resolves. Traditional abstract compositions, which do not depict natural objects, use purely visual forms of line, color

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and shape to evoke emotional and aesthetic responses, whereas Pepperell's indeterminate paintings strongly imply natural forms, while at the same time resisting easy or immediate recognition (Fig. 1). The indeterminacy effect is achieved by omitting suggestively rendering forms, such as bodies, buildings and mountains, from which visual cues might facilitate recognition (Pepperell, 2006). Recently, we have shown that when compared with representational paintings that explicitly depict objects, subjects take longer to recognize familiar objects in indeterminate art works. Moreover, representational paintings are more likely to be remembered than indeterminate compositions in a delayed memory task, suggesting that meaningful content is critical for incidental memory (Ishai, Fairhall, & Pepperell, 2007).

Object recognition is a highly developed visual skill in primates. Behavioral and electrophysiological studies in humans and monkeys have suggested that object recognition is a rapid process that can be achieved within a few hundred milliseconds (Fabre-Thorpe, Richard, & Thorpe, 1998; Rousset, Fabre-Thorpe, & Thorpe, 2002; Thorpe, Fize, & Marlot, 1996). Moreover, it has been shown that identification of objects within natural scenes is facilitated when the context is meaningful (Bar, 2004; Biederman, 1972). The process of parsing the world into meaningful objects is mediated by activation in the ventral occipitotemporal cortex, the so called “what” pathway, which is dedicated for object recognition (Haxby et al., 1994; Ungerleider & Mishkin, 1982). Recent functional brain imaging studies in humans have shown that objects and faces elicit activation in a distributed cortical network that encompasses a wide expanse of the visual ventral stream (Haxby et al., 2001; Ishai, Ungerleider, Martin, & Haxby, 2000; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Malach et al., 1995; Pietrini et al., 2004). Within the ventral stream, faces and animals evoke stronger activation in the lateral fusiform gyrus, whereas houses and tools evoke stronger activation in the medial fusiform gyrus (Aguirre, Zarahn, & D’Esposito, 1998; Chao, Haxby, & Martin, 1999; Epstein & Kanwisher, 1998; Ishai et al., 1999; Kanwisher, McDermott, & Chun, 1997). Interestingly, ambiguous figures (Andrews, Schluppeck, Homfray, Matthews, & Blakemore, 2002; Kleinschmidt, Buchel, Zeki, & Frackowiak, 1998), illusory contours (Seghier & Vuilleumier, 2006; Stanley & Rubin, 2003), binocular rivalry (Tong, Nakayama, Vaughan, & Kanwisher, 1998) and visual mental imagery (Ishai, Ungerleider, & Haxby, 2000; Mechelli, Price, Friston, & Ishai, 2004) evoke activation in object-responsive regions in extrastriate cortex, suggesting that the visual system imposes top-down interpretations on ambiguous bottom-up retinal input. Moreover, an electrophysiological study has shown an increase in neuronal activity in V4 when monkeys learned to identify degraded, indeterminate visual images, suggesting that the resolution of indeterminate pictures is mediated by an increased amount of information communicated by neurons in this region (Rainer, Lee, & Logothetis, 2004).

We have recently shown that abstract paintings evoke activation in inferior occipital gyrus, whereas portraits and landscapes evoke activation in face- and house-responsive regions in the fusiform gyrus,

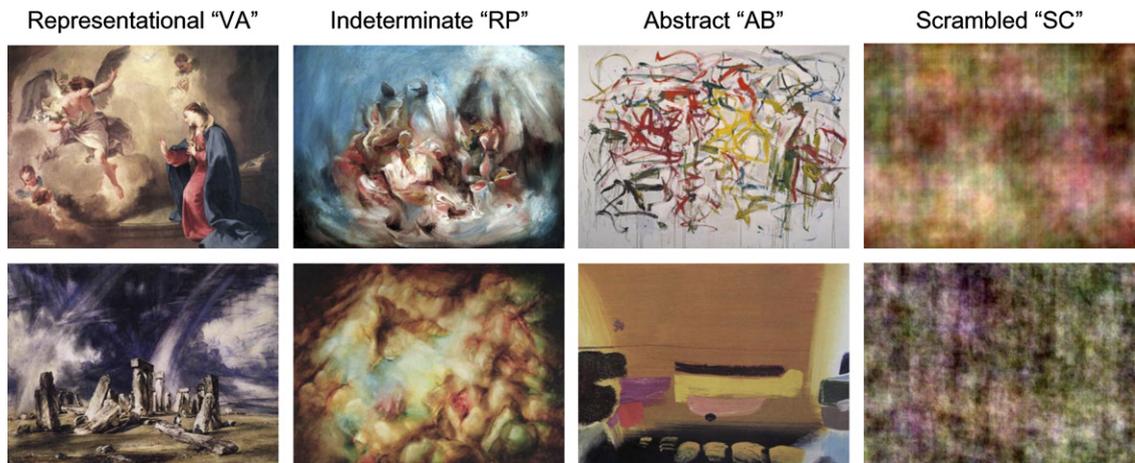


Fig. 1. Stimuli and task. Art paintings (Representational “VA”; Indeterminate “RP”; and Abstract “AB”) and Scrambled (“SC”) images used in the experiment. Each painting was presented for 3 s and subjects were instructed to report, by pressing one of two buttons, whether they recognize any familiar objects.

respectively, suggesting that activation in higher-tier, object-selective visual regions depends on meaningful, representational content (Yago & Ishai, 2006). The aim of our current study was to investigate the extent to which viewers perceive recognizable objects in art works. To that end, we used three classes of paintings: representational, which explicitly depict complex scenes with familiar objects (people, animals, landscapes, still life); indeterminate, in which familiar objects are only suggestive; and abstract, which do not depict any familiar objects (see Fig. 1). We hypothesized that subjects would rapidly recognize familiar objects depicted in representational paintings, but would be slower to report the presence or absence of recognizable objects in abstract and indeterminate paintings. Moreover, we predicted a posterior-to-anterior gradient of activation along the ventral visual pathway, with stronger response to abstract compositions in inferior occipital gyrus; stronger response to indeterminate paintings in intermediate regions in posterior fusiform gyrus; and stronger response to representational paintings in anterior fusiform gyrus. Thus, with increased recognition of familiar content in the paintings, differential activation would be observed in more anterior, higher-tier, object-selective areas. Finally, we postulated that indeterminate paintings would invoke visual imagery-related activation in parietal and prefrontal cortices.

We found activation within a distributed cortical network that includes extrastriate ventral and dorsal visual regions, as well as parietal, limbic and prefrontal regions. Consistent with our hypotheses, representational paintings with meaningful content evoked stronger activation than abstract and indeterminate paintings in the fusiform gyrus. Moreover, we found enhanced activation in the precuneus and medial frontal gyrus during the presentation of scrambled paintings. Finally, stronger activation in response to representational paintings was found in the temporoparietal junction (TPJ).

2. Methods

2.1. Subjects

Twelve right-handed subjects (five female, mean age 25 years) participated in this study. All subjects had normal or corrected to normal vision. Informed consent was obtained from all subjects and procedures were in accordance with protocols approved by the University Hospital. The subjects, students from the Neuroscience Center at the University of Zurich, had no formal art education and reported visiting art museums once a year or less. Post-scanning, all subjects filled detailed questionnaires and none of them reported recognizing any of the paintings presented during the experiment.

2.2. Stimuli and task

Stimuli were displayed with presentation (<http://www.neurobs.com>, version 9.13) and were projected with a magnetically shielded LCD video projector onto a translucent screen placed at the feet of the subject. Stimuli consisted of three classes of paintings: 52 representational paintings, in which familiar objects are depicted, by various artists (VA); 52 indeterminate paintings, in which familiar objects are suggestive, by Robert Pepperell (RP); and 52 abstract paintings, which do not familiar objects, by various artists (AB). For visual baseline we used phase scrambled images (SC), which were created by phase scrambling luminance and color information from the VA, RP and AB paintings. For each subject, four runs of 52 trials each were collected. Within each run, 13 stimuli of each painting class and 13 scrambled paintings were presented in random order. Each stimulus was presented for 3 s, and subjects were asked to quickly respond whether they recognized any familiar objects by pressing one of two buttons (1 = Yes, 2 = No). Responses were recorded via a scanner compatible response box.

2.3. Data acquisition

Data were collected using a 3T Philips Intera whole body MR scanner (Philips Medical Systems, Best, The Netherlands). Changes in blood-oxygenation level-dependent MRI signal were measured by using sensitivity encoded gradient-echo echoplanar sequence (SENSE, Pruessmann, Weiger, Scheidegger, & Boesiger, 1999) with 35 axial slices, TR = 3 s, TE = 35 ms, flip angle = 82°, field of view = 220 mm, acquisition

matrix = 80×80 , reconstructed voxel size = $1.72 \times 1.72 \times 4$ mm and SENSE acceleration factor $R = 2$. High-resolution spoiled gradient recalled echo structural images were collected in the same session for all the subjects (180 axial slices, TR = 20 ms, TE = 2.3 ms, field of view = 220 mm, acquisition matrix = 224×224 , reconstructed voxel size = $0.9 \times 0.9 \times 0.75$ mm). These high-resolution anatomical images provided detailed anatomical information for the region-of-interest analysis and were used for 3D normalization to the Montreal Neurological Institute (MNI) template.

2.4. Data analysis

Data were analyzed in SPM5 (<http://www.fil.ion.ucl.ac.uk/spm/software/spm5/>). All volumes were slice time corrected, realigned to the first volume, corrected for motion artefacts, mean-adjusted by proportional scaling, normalized into standard stereotactic MNI space 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 MNI coordinates were then converted to the Talairach space (Talairach & Tournoux, 1998).

Stimulus events were modeled using a delta function, which was convolved with a canonical hemodynamic response function to yield a regressor for each condition. Additionally, the three initial and concluding scrambled images from each run were modeled as regressors of no interest and were not included in further analysis. Regressors were entered into a GLM analysis (Friston, Holmes, Poline et al., 1995; Friston, Holmes, Worsley et al., 1995). Regions of interest (ROIs) were identified by the main effect of all paintings vs. scrambled paintings. Based on this contrast, a set of ROIs, which demonstrated a significant response to paintings ($p < .001$ in all regions and $p < .01$ in the hippocampus), were anatomically defined for each subject. These ROIs included, bilaterally, the inferior occipital gyrus (IOG), the fusiform gyrus (FG), the dorsal occipital cortex (DOC), intra parietal sulcus (IPS), hippocampus (HIP) and inferior frontal gyrus (IFG). The parameter estimates for each condition at the peak voxel within each region were extracted and used for between-subjects random-effects analyses. p Values were corrected based on the spatial extent of the activated region (see Friston, Worsley, Frackowiak, Mazziotta, & Evans, 1993).

3. Results

3.1. Behavioral data

The behavioral data recorded in the MR scanner are shown in Fig. 2. Objects were detected, on average, in 94% of the VA paintings, 36% of the RP paintings and 18% of the AB paintings. One percent of scrambled paintings received a ‘Yes’ response. All differences between conditions in the percentage of ‘Yes’ responses were significant ($p < .05$). Reaction times for ‘No’-VA responses and ‘Yes’-SC responses were omitted due to the infrequency of these responses.

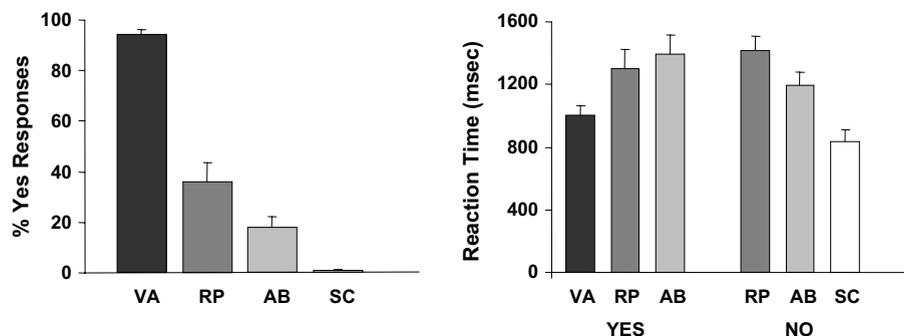


Fig. 2. Behavioral data. Mean percentage of paintings in which subjects recognized familiar objects (left), and reaction time (right) for each class of paintings. ‘Yes’-SC and ‘No’-VA reaction times were omitted due to the infrequency of these responses. Error bars indicate one standard error.

to the insufficient number of trials in these response categories. Pairwise *t*-tests revealed that ‘No’ responses to scrambled paintings were significantly faster than ‘Yes’ responses to VA paintings ($p < .005$), which were in turn faster than other responses categories ($p < .01$ in all cases). ‘No’ responses for AB paintings were significantly faster than the ‘No’ responses for RP paintings ($p < .006$) and the ‘Yes’ responses for the AB paintings ($p < .045$).

3.2. Imaging data

3.2.1. Activation evoked by art paintings

The main effect, namely responses evoked by all paintings as compared with responses evoked by the scrambled paintings, revealed significant activation within a distributed cortical network (Fig. 3). Representational, indeterminate and abstract paintings evoked activation in visual, limbic, parietal and prefrontal regions, which include the IOG and FG in the ventral stream; DOC in the dorsal stream; the hippocampus, IPS and IFG (Table 1). The ROI analysis revealed significant activation in all regions in response to all painting classes, with a tendency for enhanced responses to the VA paintings (Fig. 3). In the right FG, activation evoked by the representational paintings was significantly stronger than activation evoked by either the indeterminate ($t_9 = 2.82$, $p < .017$) or the abstract ($t_9 = 2.21$, $p < .049$) paintings. In the right hippocampus, the response evoked by the RP paintings was significantly weaker than both activation evoked by the VA ($t_6 = 2.99$, $p < .024$) and the AB paintings ($t_6 = 2.87$, $p < .028$).

3.2.2. The indeterminacy effect

In order to identify the neural correlates of object indeterminacy, we compared the response evoked by scrambled paintings, of which 99% were perceived as not containing any familiar objects, with activation evoked by the indeterminate paintings, of which 36% were perceived as containing familiar objects (see Fig. 2). This contrast (SC > RP) revealed significant clusters of activation in the precuneus (cluster size = 293, $p_{\text{corrected}} < .001$) and in the medial frontal gyrus (cluster size = 182, $p_{\text{corrected}} < .001$). Interestingly, comparing

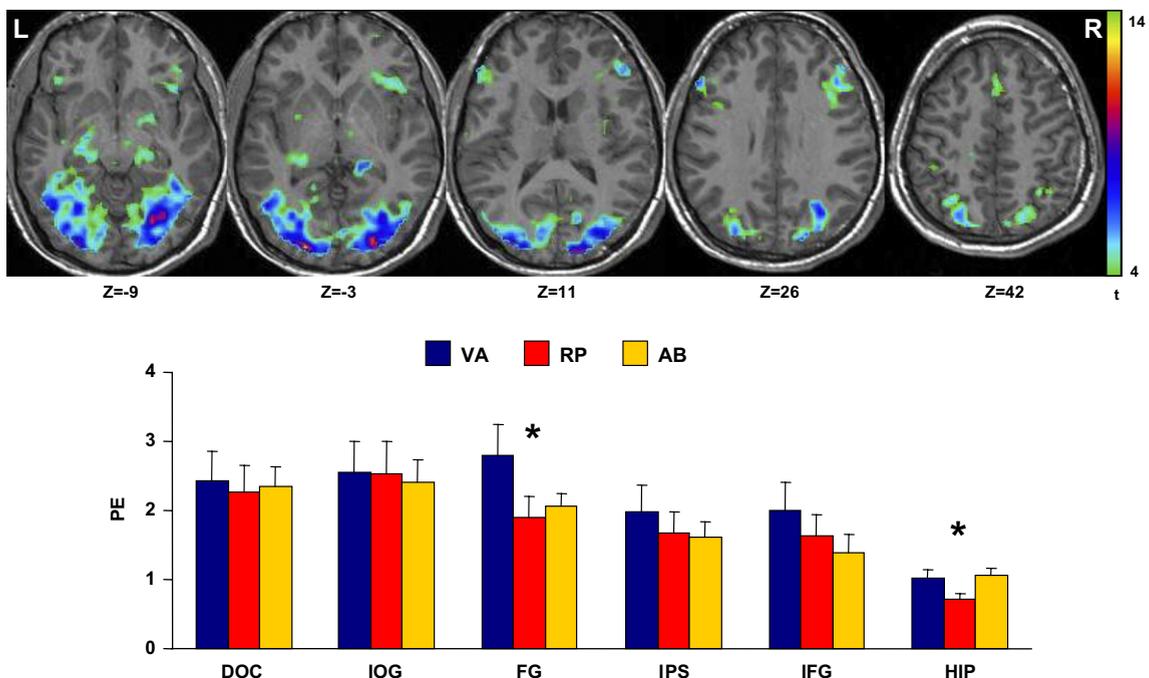


Fig. 3. Main effect. Top: group statistical maps. The axial sections depict activation evoked by all paintings vs. the scrambled paintings. Bottom: ROI analysis. Parameter estimates within each right hemisphere region were averaged across all subjects who showed activation in this region. Asterisks indicate significant effects ($p < .05$). Error bars indicate one standard error.

Table 1
Regions identified by the main effect (all paintings vs. scrambled paintings)

Regions	BA	<i>N</i>	<i>x</i>	<i>y</i>	<i>z</i>
L. DOC	18	10	−30(2)	−91(1)	11(2)
R. DOC	18	12	31(2)	−89(2)	16(2)
L. IOG	19	12	−30(2)	−85(2)	−15(2)
R. IOG	19	12	29(2)	−84(2)	−17(1)
L. FG	37	8	−35(2)	−56(2)	−21(1)
R. FG	37	10	38(2)	−57(2)	−19(1)
L. HIP		4	−22(3)	−31(1)	−3(1)
R. HIP		7	25(3)	−27(2)	−7(2)
L. IPS	7	9	−21(3)	−71(3)	49(2)
R. IPS	7	8	27(2)	−67(4)	46(2)
L. IFG	44	7	−51(2)	24(5)	21(7)
R. IFG	44	8	50(3)	26(3)	22(2)

N indicates the number of subjects who showed significant activation in each region. BA, Brodmann area. Coordinates are in the normalized space of the Talairach and Tournoux atlas. L, left; R, right. Standard error of the MEAN is indicated in parentheses.

activation evoked by the abstract and indeterminate paintings ($AB > RP$) also revealed activation within these regions, albeit in smaller clusters (Fig. 4). Contrasting the response evoked by the scrambled paintings with activation evoked by either the representational or the abstract paintings did not reveal any significant activation within these regions.

3.2.3. The effect of meaningful content

The main effect revealed that within visual, parietal and prefrontal regions the amplitude of the fMRI signal in response to VA, RP and AB paintings was very similar. In order to identify the neural correlates of meaningful content in art works we contrasted activation evoked by the representational paintings with activation evoked by the indeterminate ones (VA vs. RP). A group analysis revealed bilateral clusters of activation in the superior temporal sulcus, angular gyrus and the supramarginal gyrus ($p < .001$ uncorrected, Fig. 5). Collectively, these regions constitute the temporoparietal junction (TPJ). The spatial extent of the TPJ cluster in the right hemispheric was sufficient to survive corrections for multiple comparisons (cluster size = 40, $p_{\text{corrected}} = .001$). Interestingly, an overlapping region in the right TPJ also showed greater responses to VA than AB paintings ($p < .001$ uncorrected).

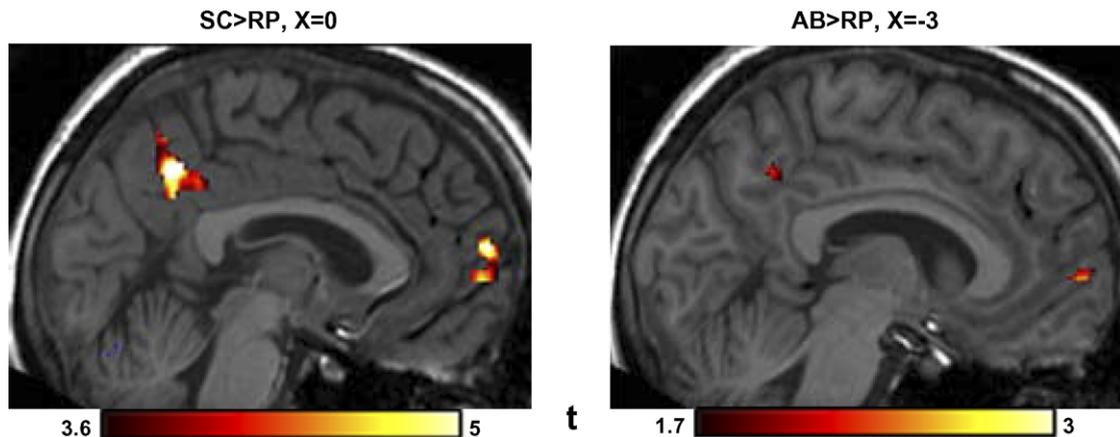


Fig. 4. The indeterminacy effect. Left: comparison of activation evoked by scrambled paintings and indeterminate paintings ($SC > RP$). The sagittal group map indicates stronger activation in the precuneus (peak voxel: $x = -0$, $y = -45$, $z = 35$) and medial frontal gyrus (peak voxel: $x = 0$, $y = 60$, $z = 9$) for scrambled paintings. Right: comparison of activation evoked by abstract paintings and indeterminate paintings ($AB > RP$). Overlapping activation was observed in the precuneus and the MFG, albeit with a reduced threshold.

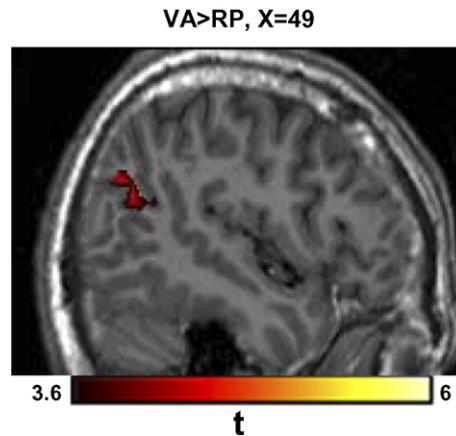


Fig. 5. Content effect. Representational paintings evoked stronger activation than indeterminate paintings (VA > RP) in the temporoparietal junction (peak voxel: $x = 50$, $y = 63$, $z = 19$).

4. Discussion

We used representational, indeterminate and abstract paintings to study the neural correlates of object indeterminacy in art compositions. Subjects rapidly recognized familiar objects in VA paintings, but showed longer reaction times to RP and AB images, both when objects were detected and when they were not recognized. These differential response latencies suggest an automatic recognition of objects when they were explicitly depicted (VA paintings), but more effortful cognitive processes when the objects were ambiguous or suggestive (RP and AB paintings). Consistent with our previous study, objects were detected in 36% of the RP paintings, but less frequently in the AB paintings (18%), reflecting the nature of RP paintings (Ishai et al., 2007). The increase in object ambiguity was also reflected in the longer time required to exclude the presence of objects in RP paintings than in AB paintings.

The main effect of visual perception of all paintings revealed significant activation within a distributed cortical network. In the visual cortex, similar responses were evoked by all paintings in extrastriate ventral and dorsal regions. These regions include the IOG and FG, where object form is processed (Epstein & Kanwisher, 1998; Haxby et al., 2001; Ishai et al., 1999; Malach et al., 1995), and the DOC, where configurational relationships are processed (Ishai et al., 1999; Ishai, Ungerleider, Martin et al., 2000). Moreover, we found activation in the IPS, which is modulated by attentional demands (Corbetta et al., 1998; Nobre et al., 1997). Our hypothesis that abstract and indeterminate paintings would evoke stronger activation in posterior and intermediate regions along the ventral stream, whereas representational paintings would evoke enhanced activation in higher-tier areas, was partially confirmed. VA paintings evoked stronger activation than RP and AB paintings in the FG, a region that responds to assorted common objects, including faces, houses, animals and tools (Aguirre, Zarahn, & D'Esposito, 1998; Chao et al., 1999; Epstein & Kanwisher, 1998; Ishai et al., 1999; Kanwisher et al., 1997; Yago & Ishai, 2006). Our results are consistent with a recent study in which enhanced activation in the FG was observed when representational paintings were compared with filtered paintings (Vartanian & Goel, 2004). The patterns of activation observed in posterior visual cortex suggest that a composite image of visual features (e.g., lines, colors and shapes), regardless of its meaningful or familiar content, is sufficient to evoke robust activation within the DOC and the IOG. The enhanced response to VA paintings in the right fusiform gyrus reflects access to stored representations of familiar objects. It has been suggested that figure-ground segmentation of visual scenes depends on perceptual grouping of image elements that belong to the same object (Roelfsema, 2006). Our findings indicate that this seemingly effortless process occurs not only with familiar objects, but also with indeterminate stimuli that do not contain real objects. It therefore seems that the primate brain is a compulsory object viewer, namely automatically segments indeterminate visual input into coherent images. It is important to note that the subjects were instructed to quickly respond if they recognized any familiar objects, but were not asked to name the objects. A naming task would likely evoke activation in more anterior temporal regions (Chao et al., 1999; Moore & Price, 1999; Price et al., 2006).

The indeterminate paintings, when compared with the representational and the abstract compositions, evoked less activation in the right hippocampus. This reduced activation may reflect the poor encoding of the RP paintings, consistent with our previous study, in which subjects recalled significantly less RP than VA paintings in a surprise memory task (Ishai et al., 2007).

To further identify the neural correlates of object indeterminacy, we compared activation evoked by scrambled paintings with activation evoked by the indeterminate paintings. We found that the scrambled paintings evoked enhanced activation in the precuneus and the MFG, regions of the “imagery network,” which mediate the generation and maintenance of mental images from long-term memory (Fletcher et al., 1995; Gardini, Cornoldi, De Beni, & Venneri, 2006; Ishai, Haxby, & Ungerleider, 2002; Ishai, Ungerleider, & Haxby, 2000; Mechelli et al., 2004). Post-scanning debriefing revealed that most subjects used mental imagery during the perception of the scrambled paintings, in an attempt to decide whether the images contained any familiar objects. In contrast, to decide whether the indeterminate paintings, which were rich with suggestive objects, contained any recognizable objects, subjects relied on visual similarity and visual associations.

A direct comparison of representational and indeterminate art works revealed significant activation in the TPJ, a region that has been implicated in exerting attentional control over switches from local to global processing (Fink et al., 1996), and the allocation of spatial attention across the visual scene (Corbetta, Kincade, Lewis, Snyder, & Sapir, 2005). The enhanced activation within the TPJ for the VA paintings reflects the binding of object form and spatial location within these cluttered visual scenes. Our findings therefore suggest that the recognition of meaningful, familiar content in art works is mediated by activation in the TPJ. Incidentally, the left TPJ was also activated by ‘beautiful’ rather than ‘neutral’ art paintings (Kawabata & Zeki, 2004). We have previously shown, however, that the aesthetic judgment of VA and RP paintings resulted in virtually identical ratings of affect (Ishai et al., 2007). It therefore seems unlikely that the stronger activation evoked by VA than RP paintings in the TPJ was merely due to their aesthetic affect.

In summary, our results show that perception of art compositions evokes activation in multiple extrastriate ventral and dorsal regions, the hippocampus, IPS and IFG. Content-related modulation in the FG reflects object perception, whereas hippocampal activation reflects memory consolidation. Imagery-related activation was observed for meaningless scrambled paintings. Finally, interpreting composite scenes relies on higher order associations in the TPJ, which links the various elements of the visual scene. Taken collectively, our results indicate that visual perception of art paintings evokes activation within a distributed cortical network that mediates higher cognitive processes.

Acknowledgments

We thank Robert Pepperell for providing us with the stimuli and for reading the manuscript. This study was supported by the Swiss National Science Foundation Grant 3200B0-105278 and by the Swiss National Center for Competence in Research: Neural Plasticity and Repair.

References

- Aguirre, G. K., Zarahn, E., & D’Esposito, M. (1998). An area within human ventral cortex sensitive to “building” stimuli: Evidence and implications. *Neuron*, *21*, 373–383.
- Andrews, T. J., Schluppeck, D., Homfray, D., Matthews, P., & Blakemore, C. (2002). Activity in the fusiform gyrus predicts conscious perception of Rubin’s vase-face illusion. *Neuroimage*, *17*, 890–901.
- Bar, M. (2004). Visual objects in context. *Nature Review Neuroscience*, *5*, 617–629.
- Biederman, I. (1972). Perceiving real-world scenes. *Science*, *177*, 77–80.
- Chao, L. L., Haxby, J. V., & Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nature Neuroscience*, *2*, 913–919.
- Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A., et al. (1998). A common network of functional areas for attention and eye movements. *Neuron*, *21*, 761–773.
- Corbetta, M., Kincade, M. J., Lewis, C., Snyder, A. Z., & Sapir, A. (2005). Neural basis and recovery of spatial attention deficits in spatial neglect. *Nature Neuroscience*, *8*, 1603–1610.
- Epstein, R., & Kanwisher, N. (1998). A cortical representation of the local visual environment. *Nature*, *392*, 598–601.

- Fabre-Thorpe, M., Richard, G., & Thorpe, S. J. (1998). Rapid categorization of natural images by rhesus monkeys. *Neuroreport*, *9*, 303–308.
- Fink, G. R., Halligan, P. W., Marshall, J. C., Frith, C. D., Frackowiak, R. S. J., & Dolan, R. J. (1996). In the brain does visual attention select the forest and the trees? *Nature*, *382*, 626–628.
- Fletcher, P. C., Frith, C. D., Baker, S. C., Shallice, T., Frackowiak, R. S. J., & Dolan, R. J. (1995). The mind's eye—precuneus activation in memory-related imagery. *Neuroimage*, *2*, 195–200.
- Friston, K. J., Worsley, K. J., Frackowiak, R. S. J., Mazziotta, J. C., & Evans, A. C. (1993). Assessing the significance of focal activations using their spatial extent. *Human Brain Mapping*, *1*, 210–220.
- Friston, K. J., Holmes, A. P., Poline, J. B., Grasby, P. J., Williams, S. C., Frackowiak, R. S., et al. (1995). Analysis of fMRI time-series revisited. *Neuroimage*, *2*, 45–53.
- Friston, K. J., Holmes, A. P., Worsley, K. J., Poline, J. P., Frith, C. D., & Frackowiak, R. S. J. (1995). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping*, *2*, 189–210.
- Gamboni, D. (2002). *Potential Images: Ambiguity and indeterminacy in modern art*. London: Reaktion Books.
- Gardini, S., Cornoldi, C., De Beni, R., & Venneri, A. (2006). Left mediotemporal structures mediate the retrieval of episodic autobiographical mental images. *NeuroImage*, *30*, 645–655.
- Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science*, *293*, 2425–2430.
- Haxby, J. V., Horwitz, B., Ungerleider, L. G., Maisog, J. M., Pietrini, P., & Grady, C. L. (1994). The functional organization of human extrastriate cortex: A PET-rCBF study of selective attention to faces and locations. *Journal of Neuroscience*, *14*, 6336–6353.
- Ishai, A., Fairhall, S. L., & Pepperell, R. (2007). Perception, memory and aesthetics of indeterminate art. *Brain Research Bulletin*, *73*, 314–324.
- Ishai, A., Haxby, J. V., & Ungerleider, L. G. (2002). Visual imagery of famous faces: Effects of memory and attention revealed by fMRI. *Neuroimage*, *17*, 1729–1741.
- Ishai, A., Ungerleider, L. G., Martin, A., & Haxby, J. V. (2000). The representation of objects in the human occipital and temporal cortex. *Journal of Cognitive Neuroscience*, *12*, 35–51.
- Ishai, A., Ungerleider, L. G., & Haxby, J. V. (2000). Distributed neural systems for the generation of visual images. *Neuron*, *28*, 979–990.
- Ishai, A., Ungerleider, L. G., Martin, A., Schouten, J. L., & Haxby, J. V. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Sciences of the United States of America*, *96*, 9379–9384.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, *17*, 4302–4311.
- Kawabata, H., & Zeki, S. (2004). Neural correlates of beauty. *Journal of Neurophysiology*, *91*, 1699–1705.
- Kleinschmidt, A., Buchel, C., Zeki, S., & Frackowiak, R. S. (1998). Human brain activity during spontaneously reversing perception of ambiguous figures. *Proceedings of the Royal Society B: Biological Sciences*, *265*, 2427–2433.
- Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., et al. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *92*, 8135–8139.
- Mechelli, A., Price, C. J., Friston, K. J., & Ishai, A. (2004). Where bottom-up meets top-down: neuronal interactions during perception and imagery. *Cerebral Cortex*, *14*, 1256–1265.
- Moore, C. J., & Price, C. J. (1999). A functional neuroimaging study of the variables that generate category-specific object processing differences. *Brain*, *122*, 943–962.
- Nobre, A. C., Sebestyen, G. N., Gitelman, D. R., Mesulam, M. M., Frackowiak, R. S., & Frith, C. D. (1997). Functional localization of the system for visuospatial attention using positron emission tomography. *Brain*, *120*, 515–533.
- Pepperell, R. (2006). Seeing Without Objects: Visual Indeterminacy and Art. *Leonardo*, *39*, 394–400.
- Pietrini, P., Furey, M. L., Ricciardi, E., Gobbini, M. I., Wu, W. H., Cohen, L., et al. (2004). Beyond sensory images: Object-based representation in the human ventral pathway. *Proceedings of the National Academy of Sciences of the United States of America*, *101*, 5658–5663.
- Price, C. J., McCrory, E., Noppeney, U., Mechelli, A., Moore, C. J., Biggio, N., et al. (2006). How reading differs from object naming at the neuronal level. *NeuroImage*, *29*, 643–648.
- Pruessmann, K. P., Weiger, M., Scheidegger, M. B., & Boesiger, P. (1999). SENSE: Sensitivity encoding for fast MRI. *Magnetic Resonance in Medicine*, *42*, 952–962.
- Rainer, G., Lee, H., & Logothetis, N. K. (2004). The effect of learning on the function of monkey extrastriate visual cortex. *PLoS Biology*, *2*, 275–284.
- Roelfsema, P. R. (2006). Cortical algorithms for perceptual grouping. *Annual Review of Neuroscience*, *29*, 203–227.
- Rousselet, G. A., Fabre-Thorpe, M., & Thorpe, S. J. (2002). Parallel processing in high-level categorization of natural images. *Nature Neuroscience*, *5*, 629–630.
- Seghier, M. L., & Vuilleumier, P. (2006). Functional neuroimaging findings on the human perception of illusory contours. *Neuroscience and Biobehavioral Review*, *30*, 595–612.
- Stanley, D. A., & Rubin, N. (2003). fMRI activation in response to illusory contours and salient regions in the human lateral occipital complex. *Neuron*, *37*, 323–331.
- Talairach, J., & Tournoux, P. (1998). *Co-planar stereotaxic atlas of the human brain*. New York: Theme Medical.
- Thorpe, S., Fize, D., & Marlot, C. (1996). Speed of processing in the human visual system. *Nature*, *381*, 520–522.

- Tong, F., Nakayama, K., Vaughan, J. T., & Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron*, *21*, 753–759.
- Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In *Analysis of visual behavior* (pp. 747–764). Cambridge, MA: MIT Press.
- Vartanian, O., & Goel, V. (2004). Neuroanatomical correlates of aesthetic preference for paintings. *Neuroreport*, *15*, 893–897.
- Yago, E., & Ishai, A. (2006). Recognition memory is modulated by visual similarity. *Neuroimage*, *31*, 807–817.