

Art Compositions Elicit Distributed Activation in the Human Brain

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*"Indeed, the true miracle of the language of art is not that it enables the artist to create the illusion of reality. It is that under the hands of a great master the image becomes translucent. In teaching us to see the visible world afresh, he gives us the illusion of looking into the invisible realms of the mind - if only we know, as Philostratus says, how to use our eyes."*¹

With the advent of functional brain imaging techniques, especially functional Magnetic Resonance Imaging (fMRI), a technique that permits the localization of regions that are activated during cognition, with fine spatial and temporal resolutions (millimeters and seconds, respectively), neuroscientists routinely investigate the neural mechanisms that mediate our experience of viewing and enjoying art. In order to "see the visible world afresh," we need to use not only our eyes, but importantly, also our brain. In his book "Inner Vision", Zeki suggested that both the nervous system and artists try to understand the essential visual attributes of the world. In the visual cortex, information is decomposed into such attributes as color, luminance and motion. Similarly, many artists isolate and enhance such visual attributes, in their work. Mondrian and Calder, for example, emphasized color and motion, respectively². Although many artists have uncovered visual "modules" that are anatomically and functionally segregated in the brain, in my opinion Zeki's parallelism approach, although compelling, is over simplified. When we view paintings, not only does our brain analyze the visual scene to identify familiar objects, but we also have an emotional reaction and we immediately assign aesthetic value to these paintings. Recent studies of art perception and memory suggest that when confronted with abstract or indeterminate art compositions, the human

brain automatically solves the perceptual dilemma by generating predictions about their content based on familiar associations stored in memory. In this chapter, I will argue that viewing art is not a passive process, but rather a dynamic cognitive function that engages distributed cortical networks activated during the allocation of attention, mental imagery, and retrieval from memory. My fMRI studies provide, therefore empirical evidence for Gombrich's suggestion that we use schemas when we view works of art, namely we use stored structures of knowledge in order to form expectations (see also Chapter 1).

Brain evolution and the origin of art

The human brain has evolved over a period of 6 million years from the common ancestor of humans, apes and other simians, to the appearance of *Homo Sapiens Sapiens* about 100,000 years ago³. Over that time, the architecture of the brain evolved to adapt to new functions and behaviours in response to complex encounters in the environment, while the mind formed an internalized model of this environment. Early humans made tools and socialized as the brain grew larger and its volume increased from 400 grams to 1400 grams. Social interactions stimulated an ability to imagine the mind of others in order to predict their behaviour. Language appeared about 250,000 years ago and its vocabularies and syntax became more sophisticated with time. Humans use language in distinctively different ways from the alarm calls used by animals because we have syntax, namely we arrange words grammatically and embed qualifying clauses in sentences to demonstrate complex understanding of time, causation, connections and relationships. Language is a sophisticated form of symbolic communication that allowed early humans to convey concrete, detailed information and abstract concepts and to cooperate and plan for the future, in order to ensure their survival.

It is unclear why, when and how self-consciousness emerged, but around 135,000 years ago humans began to produce something different and exceptional: works of art. After using stones for tool-making for millions of years, humans start using bones and shells which they fashion into ornaments⁴. Some 30,000 years ago, cave paintings and ornamental sculptures began to appear at different sites across the world. Early visual art is surprisingly representational and informative. The famous Chauvet cave paintings are

evidence of extraordinary figurative skill in depicting three-dimensional animals alive with movement, which were created with a distinctive individual style. Making sophisticated tools and using symbols both require the capacity to hold an abstract concept in one's mind and to impose a predetermined form on raw material based on an abstract mental template. In his book, Mithen proposes five properties for a definition of art in prehistory: like language, it contains symbols that are arbitrary in relation to their referents; it is created with the intention of communication; it operates outside the here and now of space and time; the meaning of symbols can be variable between individuals and cultures, or may carry multiple meaning; and the same symbols may vary as a result of individual mark making³. Symbolic communication likely had an evolutionary advantage: it served as social glue that helped tribes of early humans to survive and reproduce. Art, from the prehistoric ornaments to Duchapmp's Fountain, is therefore a medium intended to communicate meaning⁵. Although it is widely accepted that art is a symbolic language, some challenge this notion. Based on the striking similarity in content and style of the cave art and the drawings of Nadia, an autistic girl who did not acquire spoken language but had an exceptional graphic ability, Humphrey argued that the naturalistic depictions are the result of lack of normal language development, in particular naming of animals and objects⁶. If indeed, as Humphrey suggests, language and graphic skills are partly incompatible, one would expect some anatomical and functional changes in the brain of children who can draw realistic animals from memory but cannot speak.

The creative brain

What is the neural basis of creativity? Do artists, with their unique ability to visualize and their imaginative and technical skills, have a “special” brain? With the advent of functional brain imaging techniques, such empirical questions can be routinely investigated. It is important to note, however, that most functional brain imaging studies of creativity have focused on creative problem solving or on the brain of musicians and only a very few have compared visual artists with non-artists. Converging evidence suggests that the creative brain is a result of right hemisphere specialization, which is manifested by anatomical changes in cortical thickness or volume of gray matter, and functional changes, i.e., differential patterns of neuronal activity. For example, when subjects solved verbal problems that required an insight, the “Aha!” moment was accompanied by increased activation, as measured with fMRI, in the anterior superior temporal gyrus, and a sudden burst of high-frequency (gamma-band) neural activity, as measured with EEG, in the same brain area, which was detected 0.3 seconds prior to the insight⁷. This distinct pattern of neural activity in the right anterior temporal region suggests that creative solutions require the integration of information across distant lexical or semantic relations, which enable seeing the problem in a new light.

The opportunity to scan the brains of living musicians revealed several structural and functional changes in their brain. Musicians are therefore an excellent model for brain plasticity. Recent findings suggest that musicians have more gray matter than non-musicians in Heschl’s gyrus, the region in the cerebral cortex that first receives auditory input⁸. Structural and functional specializations have been demonstrated across several

sensory, motor and higher order association areas. These specializations are often instrument-specific and correlate with aspects of the training history supporting the view that they are the result, rather than the cause, of skill acquisition⁹.

In some studies, artists were compared with non-artists while performing various cognitive tasks. Eye-movement recordings have shown that artists view pictures differently from laymen: they spend more time scanning structural and abstract features, whereas artistically untrained subjects look more at human features and objects¹⁰. A series of studies with the British portrait artist Humphrey Ocean have shown that when he draws, the fixations of his eyes were twice the duration of those when he was not drawing. Moreover, fMRI scans of his brain while he viewed faces revealed, relative to non-artists, decreased activation in the “fusiform face area”, a region in visual cortex that responds more to faces than to common objects, and increased activation in prefrontal cortex. These findings suggest that the artist processes faces more efficiently and employs higher cognitive functions, such as associations and motor planning¹¹.

It is important to emphasize that despite the accumulating evidence for neuroanatomical changes, it is currently unknown what brain mechanisms enable gifted individuals to create art. The focus of my scientific research is not the artist, but, rather, the naïve observer. The main empirical question that interests me is how the brain interprets and experience paintings, especially when the content is hardly recognizable? In my frequent visits to museums and art galleries across the world, when confronted with abstract and indeterminate paintings, I often find myself pondering the content of these paintings and

search for familiar, recognizable visual forms. In an attempt to resolve the perceptual dilemma, I turn to the title, but alas many modern paintings come untitled or with meaningless titles. Inspired by my personal experience, I conducted a series of behavioural and fMRI studies, in which the following issues were addressed: how does the brain processes ambiguous paintings? Does aesthetic judgment depend on familiar content? Do titles affect the perception of art? Can training change our perception of art? In this chapter, I describe how visual information is represented in the brain, what happens in our brain when we imagine or retrieve from memory pictures of faces and objects, how the brain solves visual indeterminacy, and how training changes the way naïve observers view Cubist paintings.

How do we perceive and imagine faces and objects?

The ability to recognize objects in the world is a highly developed visual skill in primates and significant cortical resources are dedicated to the processing of visual information. Behavioral and electrophysiological studies in humans and monkeys suggest that object recognition is a rapid process that can be achieved within a few hundred milliseconds¹². Moreover, identification of objects within natural scenes is facilitated when the context is meaningful, that is, it is more likely to find a tea cup in the kitchen than in the shower¹³⁻¹⁴. 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 to object recognition¹⁵⁻¹⁶. 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 stream¹⁷⁻¹⁹. Within the ventral stream, faces and

animals evoke stronger activation in the lateral fusiform gyrus, a region along the ventral visual pathway (see Chapter 1), whereas houses and tools evoke stronger activation in the medial fusiform gyrus^{17, 20-22}. Interestingly, ambiguous figures²³, illusory contours²⁴ and binocular rivalry²⁵, also evoke activation in object-responsive regions in the visual cortex, suggesting that the visual system imposes top-down (namely prior knowledge) interpretations on ambiguous bottom-up (namely sensory) retinal input (some examples are illustrated in Chapter 1).

Visual imagery is the ability to generate percept-like images in the absence of retinal input and therefore is a vivid demonstration of retrieving pictorial information from memory. The subjective similarity of seeing and imagining suggests that perception and imagery share common internal representations. Psychophysical and brain imaging studies have demonstrated functional similarities between visual perception and visual imagery, to the extent that common mechanisms appear to be activated by both²⁶⁻³⁰. Numerous neuroimaging studies have shown that visual imagery, like visual perception, evokes activation in occipito-parietal and occipito-temporal visual association areas³¹. In some imagery studies, the primary visual cortex was activated³²⁻³³, suggesting that the generation of mental images may involve sensory representations at the earlier processing stages in the visual pathway. Studies of patients with brain damage have demonstrated a dissociation of visual-object and visual-spatial imagery³⁴, indicating that different parts of the visual system mediate “where” and “what” imagery, a dissociation that parallels the two anatomically distinct visual systems proposed for visual perception¹⁵. Although many studies have focused on the overlap and similarities between perception and

imagery, the subjective experience of imagining and seeing is clearly different. It has been shown that during visual imagery, deactivation in auditory cortex is negatively correlated with activation in visual cortex and with the score of subjective vividness of visual imagery. Thus, to generate vivid mental images, the brain needs to filter out irrelevant sensory information³⁵.

In a series of fMRI, studies we compared perception of faces and objects with visual imagery of faces and objects. Subjects viewed pictures of faces, houses or chairs or imagined familiar faces, houses and chairs. During visual imagery, object-specific patterns of activation were found, but this activity was restricted to small sectors of the regions that responded differentially during perception. The generation of mental images of familiar faces from long-term memory evoked activation within small subsets of the lateral fusiform gyrus, a face-responsive region, whereas generating mental images of houses and chairs evoked activation within subsets of the medial fusiform and inferior temporal gyri, respectively³⁶. Similarly, studies in non-human primates indicate that the temporal lobe is the memory storehouse for visual representations of complex stimuli³⁷. Visual imagery also evoked activation within a network of parietal and frontal regions, that include the precuneus, intraparietal sulcus and inferior frontal gyrus, regions that were implicated in various attention and retrieval from episodic memory tasks³⁸⁻³⁹. These findings suggest that retrieval of content-specific memory traces, stored in the ventral pathway, is top-down controlled by a parieto-frontal network that mediates the generation and maintenance of mental images³⁶.

We then asked how these visual, parietal and prefrontal cortices are connected⁴⁰. Analysis of effective connectivity among these cortical regions revealed that dynamic neuronal interactions between occipito-temporal, parietal and frontal regions are task- and stimulus-dependent. Sensory representations of faces and objects in ventral extrastriate cortex are mediated by bottom-up mechanisms arising in early visual areas during perception, and top-down mechanisms originating in the prefrontal cortex during imagery. Additionally, non-selective, top-down processes, originating in superior parietal areas, contribute to the generation of mental images and their maintenance in the “mind’s eye”⁴¹.

Face recognition is a highly developed skill in primates and the cognitive development of face perception suggests a special status for face processing. The recognition of facial identity is based on invariant facial features, whereas animated aspects of the face, such as speech-related movement and expression, contribute to social communication. When looking at faces, we rapidly perceive the gender, expression, age and mood. Processing information gleaned from the faces of others, therefore, requires the integration of activity across a network of cortical regions. Converging empirical evidence suggests that face perception is mediated by activation within a distributed neural system⁴²⁻⁴⁵. The cortical network for face perception includes regions along the ventral pathway (the inferior occipital gyrus and lateral fusiform gyrus), which process the identification of individuals²⁰; regions along the dorsal pathway (the superior temporal sulcus), where gaze direction and speech-related movements are processed⁴⁶; limbic regions (the amygdala and insula), where facial expressions are processed⁴⁷⁻⁴⁸; frontal regions (the

inferior frontal gyrus), where semantic aspects are processed^{36, 49}, and regions of the reward circuitry, including the nucleus accumbens and orbitofrontal cortex, where facial beauty and sexual relevance are assessed⁵⁰⁻⁵³.

Famous faces represent a special class of stimuli because they are highly associated with rich pictorial and contextual information (e.g., Angelina Jolie's face elicits associations about her appearance in various movies, her liaison with Brad Pitt, her children and her humanitarian work in Africa). When subjects view faces of contemporary Hollywood celebrities, activation is found in the inferior occipital gyrus, lateral fusiform gyrus, superior temporal sulcus, and amygdala, regions of the distributed network that mediates face perception^{42-43, 54}. Interestingly, when famous faces are compared with unfamiliar faces, activation is found in the parahippocampal cortex, a region that mediates contextual associations⁵⁵. When subjects generate mental images of famous faces, activation is observed in small subsets of these face-responsive regions. Moreover, visual imagery of famous faces activates a network of regions that includes the calcarine, precuneus, hippocampus, intraparietal sulcus and inferior frontal gyrus⁵⁶. Taken collectively, these studies suggest that visual mental imagery is a multi-component cognitive process that requires re-activation of specific representations stored in the visual cortex and their maintenance in the "mind's eye". It is therefore not surprising that the 'imagery network' comprises parietal and frontal regions that also mediate attention and memory retrieval. We have recently discovered that viewing indeterminate art compositions also elicits activation within these imagery-related regions⁵⁷.

Representational paintings and recognition memory

Learning about a new category of stimuli requires experience with multiple instances that define that category. For example, encounters with very few paintings from Picasso's "Blue Period" is sufficient for the correct categorization of a new, never-seen before, Blue Period painting. As category learning and recognition memory require matching novel items with stored ones, we hypothesized that both are mediated by activation in a distributed cortical network, and used event-related fMRI to test whether matching between novel exemplars and familiar prototypes depends on their visual similarity. Our experimental approach combined explicit category learning with a recognition memory task, and an original set of stimuli, namely art compositions by painters with a unique style: portraits by Modigliani and Renoir, landscapes by Pissarro and Van Gogh, and abstract paintings by Kandinsky and Miro. In the training session, subjects were told that paintings from each artist belonged to a category of paintings with a characteristic signature and were instructed to learn and memorize these prototypes. Four days later, in the fMRI test session, subjects were presented with the familiar prototypes and with new exemplars and indicated whether they had seen these pictures before. The new exemplars were either visually similar to the prototypes, somewhat similar (ambiguous), or different (Figure 1). We predicted fast and accurate responses to the new, dissimilar exemplars, and slower, less accurate responses to the new, similar and ambiguous exemplars, due to their visual resemblance to the prototypes. Moreover, we predicted that activation in the visual cortex and in parietal and prefrontal regions would be modulated by the degree of visual similarity, and expected reduced activity with decreased visual similarity between the new exemplars and the familiar prototypes.

Our results show that, on average, 72% of the prototypes were correctly recognized and that responses to the novel items were faster and more accurate with decreased similarity to the prototypes⁵⁸. In the visual cortex, the paintings evoked activation in face- and object-selective regions, where familiar prototypes elicited stronger activation than the new exemplars. Consistent with our hypothesis, in the intraparietal sulcus and superior parietal lobule, responses evoked by new exemplars were reduced with decreased similarity to the prototypes. In memory-related areas, two patterns of activation were observed: in the caudate, insula, and anterior cingulate cortex, the familiar prototypes elicited stronger activation than the new items, whereas in the precuneus, superior temporal and superior frontal gyri the new, visually different exemplars evoked stronger activation. Finally, in the hippocampus, the similar items evoked weaker activation than the other novel exemplars. These findings suggest that recognition memory is mediated by activation in a cortical network that includes regions in visual cortex where stimulus-specific representations are stored, attention-related areas where visual similarity to familiar prototypes is detected, and memory-related areas where new items are classified as a match or a mismatch based on their similarity to familiar prototypes⁵⁸.

Our recognition memory task required subjects to simply report whether a painting was old or new. We did not address the issue of memory processes, namely to what extent the subject's decision was based on recollection, namely the retrieval of specific information about a past experience, or familiarity, namely a sense that an event has been previously experienced. We therefore designed a new event-related fMRI study to investigate whether recollection- and familiarity-based memory decisions are modulated

by the degree of visual similarity between old and new paintings. Subjects viewed, in the MR scanner, portraits, landscapes and abstract paintings and had to decide whether each painting contained a flower. Ten minutes later, they received a surprise memory test, in which the old paintings were randomly presented with new paintings that were either visually similar to or visually different from the old ones. Subjects had to decide whether they remember the picture, the picture looks familiar, or whether it's a new picture they've never seen before. Consistent with our prediction, subjects were significantly faster and more accurate at detecting new, visually different paintings than new, visually similar ones. The proportion of false alarms, namely 'remember' and 'know' responses to new paintings, was significantly reduced with decreased visual similarity. The retrieval task evoked activation in multiple visual, parietal and prefrontal regions, within which 'remember' judgments elicited stronger activation than 'know' judgments. New, visually different paintings evoked weaker activation than new, visually similar items in the intraparietal sulcus. Contrasting recollection with familiarity revealed activation predominantly within the precuneus, where the BOLD response elicited by recollection peaked significantly earlier than the BOLD response evoked by familiarity judgments (Figure 1). These findings suggest that successful memory retrieval of pictures is mediated by activation in a distributed cortical network, where memory strength is manifested by differential hemodynamic profiles. Recollection- and familiarity-based memory decisions may therefore reflect strong memories and weak memories, respectively⁵⁹.

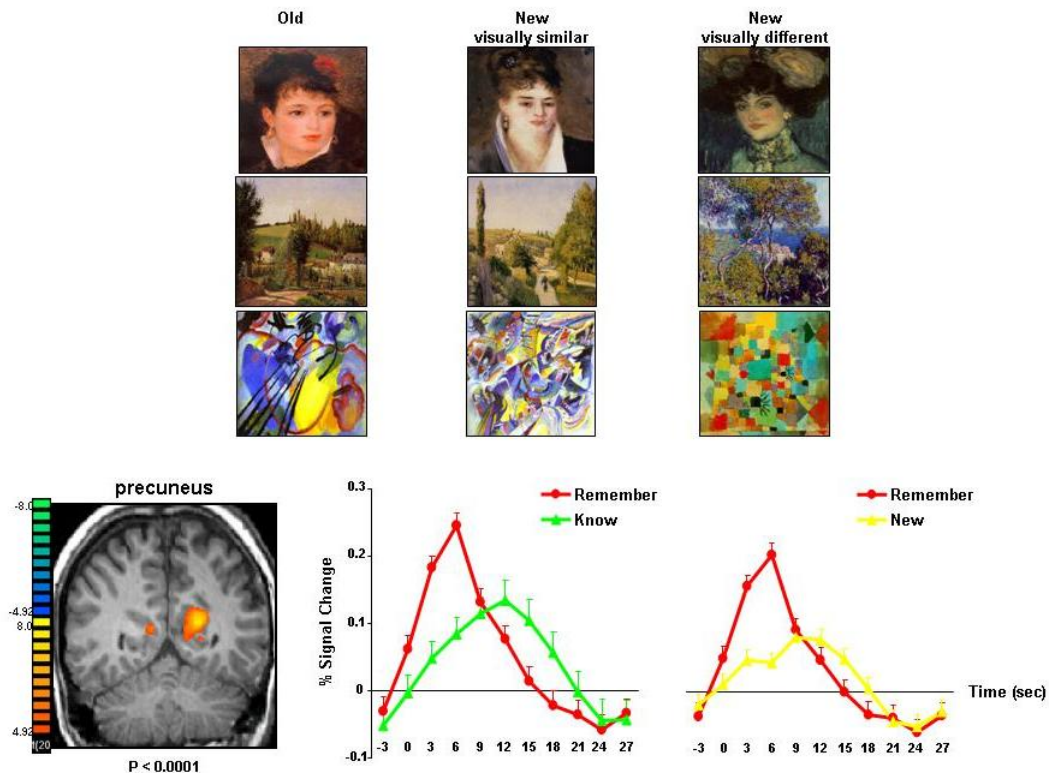


Figure 1: Recollection and familiarity reflect memory strength.

Subjects performed a flower detection task on portraits, landscapes and abstract paintings, and 10 minutes later were surprised with a memory test. The previously seen paintings (“old”) were presented with new paintings that were either visually similar to or visually different from the old ones. For each painting, subjects had to report whether they remember it, it looks familiar, or it’s new. Activation in the precuneus showed that correctly remembered old paintings evoked stronger activation than both paintings that looked familiar and new, never seen before paintings. It therefore seems that recollection reflects strong memories, whereas familiarity reflects weak memories.

Visual indeterminacy and the brain

Visual indeterminacy occurs when we 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, motion) become dissociated from the semantic aspects (association, meaning, 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'⁶⁰, 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 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 (Figure 2). The indeterminacy effect is achieved by omitting suggestively rendering forms, such as bodies, buildings and mountains, from which visual cues might facilitate recognition⁶¹.

In collaboration with Pepperell, we designed a series of new studies in order to investigate the indeterminacy effect. In a behavioral study, subjects performed object recognition and judgment of aesthetic affect tasks while viewing representational paintings by various artists and indeterminate paintings by Pepperell. Response latencies were significantly longer for indeterminate images and subjects perceived recognizable

objects in 24% of these paintings. Although the aesthetic affect rating of all paintings was similar, reaction times for the indeterminate paintings were significantly longer. A surprise memory test revealed that more representational than indeterminate paintings were remembered and that affective strength increased the probability of subsequent recall, suggesting that meaningful content is critical for incidental memory. These findings show that perception and memory of art depend on semantic aspects, whereas aesthetic affect depends on formal visual features. The longer latencies associated with indeterminate paintings reflect the underlying cognitive processes that mediate object resolution. Indeterminate art works therefore comprise a rich set of stimuli with which the neural correlates of visual perception can be investigated⁶².

We then conducted an fMRI study, in which subjects performed an object recognition task on 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 (Figure 2). 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, such that 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. Our subjects rapidly recognized familiar

objects in representational paintings, but showed longer reaction times to indeterminate and abstract images. These differential response latencies suggest an automatic recognition of objects when they were explicitly depicted, but required more effortful cognitive processes when the objects were ambiguous or suggestive⁵⁷. All paintings evoked activation within a distributed cortical network that included regions in the visual cortex, as well as parietal, limbic and prefrontal regions (Figure 2). Consistent with our hypotheses, representational paintings with meaningful content evoked stronger activation than abstract and indeterminate paintings in the fusiform gyrus, a region that responds to assorted common objects, including faces, houses, animals and tools^{17, 19, 22}. Our results are consistent with a recent study in which enhanced activation in the fusiform gyrus was observed when representational paintings were compared with filtered paintings⁶³. The indeterminate paintings, when compared with the representational and the abstract compositions, evoked less activation in the right hippocampus⁵⁷. This reduced activation may reflect the poor encoding of the indeterminate paintings, consistent with our previous study, in which subjects recalled significantly fewer indeterminate than representational paintings in a surprise memory task⁶².

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 medial frontal gyrus, regions of the “imagery network” that mediate the generation and maintenance of mental images from long-term memory^{36, 38, 41, 56}. Post-scanning

debriefing revealed that most subjects used mental imagery during the perception of the scrambled paintings, in order 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 temporo-parietal junction (TPJ), a region that has been implicated in exerting attentional control over switches from local to global processing⁶⁴, and the allocation of spatial attention across the visual scene⁶⁵. The enhanced activation within the TPJ for representational paintings reflects the binding of object form and spatial location within these cluttered visual scenes. Thus, 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’ paintings⁶⁶.

Our fMRI study shows that perception of art compositions evokes activation in multiple visual regions, the hippocampus, intraparietal sulcus and inferior frontal gyrus. Content-related modulation in the fusiform gyrus reflects object perception, whereas hippocampal activation reflects memory consolidation. Imagery-related activation was observed for scrambled paintings. Finally, interpreting composite scenes relies on higher order associations in the TPJ, which links the various elements of the visual scene. It therefore seems that the human brain is a compulsory object viewer, which automatically segments indeterminate visual input into coherent images. To resolve the visual indeterminacy,

higher cognitive functions, such as attention, visual imagery and memory retrieval, are recruited.

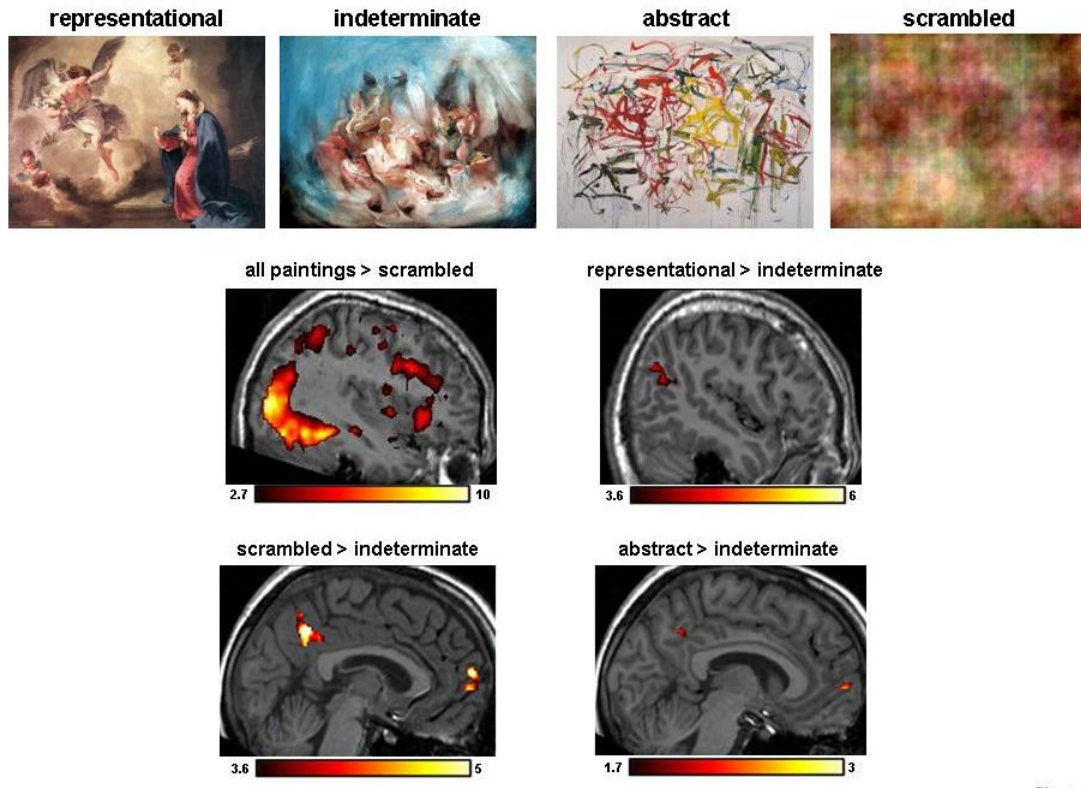


Figure 2: Activation evoked by paintings.

Viewing paintings as compared with scrambled pictures elicits activation in a distributed network of visual, limbic, parietal and frontal regions. Comparing representational with indeterminate paintings revealed activation in the temporoparietal junction, a region that mediates the allocation of spatial attention across visual scenes. Comparing scrambled pictures with indeterminate paintings and abstract paintings with indeterminate ones reveal activation in the precuneus and medial frontal gyrus, regions that mediate the generation and maintenance of mental images from long-term memory.

Object recognition in Cubist paintings

To the naïve observer, Cubist paintings contain geometrical forms in which familiar objects are hardly recognizable, even in the presence of a meaningful title. In Cubist artworks, objects are broken up, analyzed, and re-assembled to produce abstracted forms, which often depict the same objects from different viewing points. We conducted a new study to test the extent to which a short training session about Cubism would facilitate object recognition in paintings by Picasso, Braque and Gris (Figure 3). We hypothesized that subjects who received training would recognize familiar objects faster than control subjects, and would exhibit stronger activation in object-responsive and attention-related regions. Our subjects, students from the University of Zurich, had no formal art education and reported visiting art museums once a year or less. A meaningful title or the word “untitled” appeared before each Cubist painting and subjects had to answer the question “Do you recognize any familiar objects?” by pressing one of two buttons (Yes/No), then the question “How many objects did you recognize?” by pressing one of four buttons to indicate “0”, “1”, “2” or “3 or more” objects. Thirty minutes before scanning, half the subjects received a short training session, during which they were presented with information about Cubism, viewed examples of Cubist paintings, and practiced recognizing familiar objects in these paintings.

Relative to the control group, trained subjects recognized significantly more objects in the paintings and their response latencies were significantly shorter. Moreover, trained subjects took longer to report not recognizing any familiar objects in the paintings. Cubist paintings evoked activation in a distributed cortical network that included extrastriate,

parietal and prefrontal regions. Within the parahippocampal cortex, trained subjects showed a significantly larger spatial extent of activation and a parametric increase in the amplitude of the fMRI signal as a function of the number of objects they recognized (Figure 3). We also found that in trained subjects, the longer response latencies associated with failing to recognize familiar objects were correlated with activation in a fronto-parietal network that mediates spatial attention⁶⁷.

The most surprising and intriguing finding in our study is the enhanced activation in the parahippocampal cortex of trained subjects. This region, implicated in the representation and processing of spatial navigation information⁶⁸, episodic memory⁶⁹ and remote spatial memories⁷⁰, is a major node in the cortical network for contextual associations⁵⁵. Associations are formed over time, when repeated patterns and statistical regularities are extracted from the environment and stored in memory. It has been recently suggested that the role of associations is to generate predictions about the immediate future in order to guide behaviour⁷¹. It is highly likely that due to the short training session, our subjects used contextual associations to perform the tasks. Importantly, our findings provide empirical evidence for Bayesian analysis, which was proposed as a model for object perception⁷² and evoked cortical responses⁷³⁻⁷⁴. According to the Bayes perspective, the short training session enabled our subjects to match the indeterminate visual input with their top-down predictions. It is reasonable to assume that trained subjects were more likely than control subjects to suppress errors and establish a consensus between the actual bottom-up input and the top-down prediction. Thus, minimizing prediction error resulted in faster recognition of more familiar objects in Cubist paintings.

The extent to which titles do or should influence the perception of meaning and the aesthetic impression of art compositions is contentious. In art theoretical terms, critics of a formalist persuasion claim that titles are merely ‘identification tags’ that should not affect the viewer’s reading of the work. Others, however, claim titles function as guides to interpretation and provide important contextual cues to engage the attention of the viewer^{1, 75}. Empirical evidence suggests that titles influence both the understanding and the appreciation of paintings⁷⁶. In a compelling example of the top-down effects of titles on art perception, viewers’ description of the content of paintings varied according to the title (e.g., “Agony” vs. “Carnival”) they were presented with⁷⁷. In our experiment, Cubist paintings were preceded by their meaningful title or by the word “Untitled”. We found that meaningful titles facilitated object recognition, but only in trained subjects. Thus, relative to control subjects, trained subjects reported recognizing more familiar objects in paintings with meaningful titles. These findings suggest that meaningful titles can provide the top-down solution for ambiguous visual input, but only when prior knowledge or experience exists. Taken together, these observations suggest that recognition of familiar content in art works is a skill acquired through training.

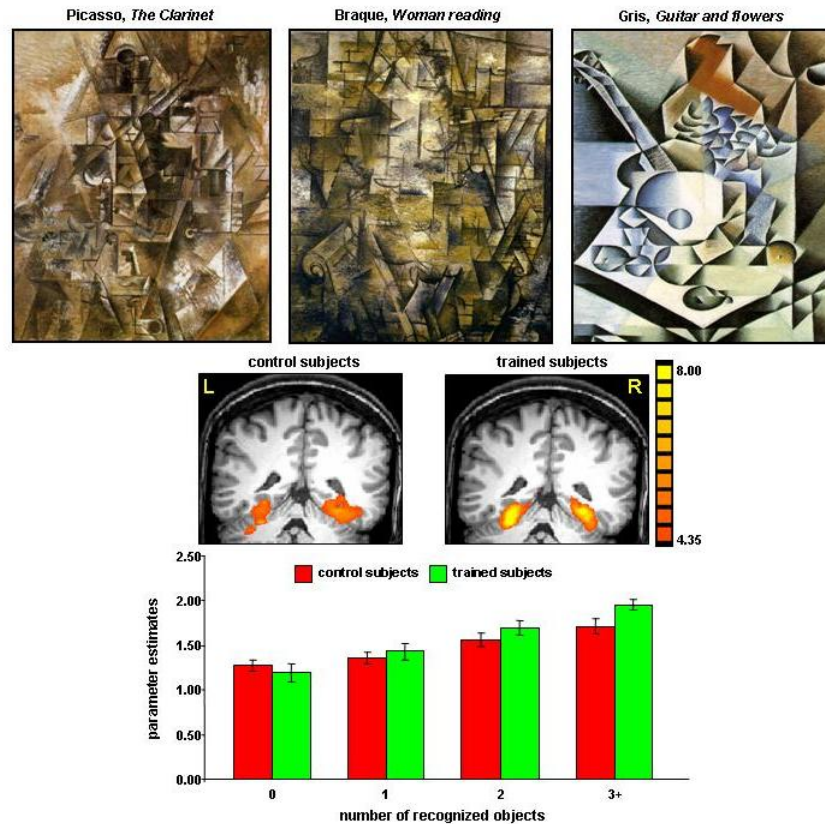


Figure 3: Training facilitates object recognition in Cubist paintings.

Subjects performed an object recognition task on Cubist paintings and indicated how many objects they recognized. Relative to the control group, the subjects who received a short training session on Cubism reported seeing more objects, activation in their parahippocampal cortex, a region that mediate contextual associations, was significantly stronger, and they showed parametric increase in the amplitude of the fMRI signal as a function of the number of objects they recognized.

Summary

Using fMRI while subjects performed object recognition and memory retrieval tasks with various classes of paintings, we have shown that the perceptual experience of art works is not a mere bottom-up process of visual analysis, but, rather, a higher cognitive function that requires top-down mechanisms such as mental imagery, memory retrieval, and contextual associations. The human brain is not a passive viewer of works of art, but a dynamic interpreter that constantly generates predictions about the content and its meaning based on previous encounters with similar visual input. Understanding the content of modern paintings is an acquired, context-dependent skill. It is perhaps not surprising that our emotional response to works of art is also influenced by knowledge and context, as suggested by recent studies of aesthetic judgment of paintings⁷⁸. If indeed art was evolved as a medium for communication by symbols, it seems that with time, as these non-linguistic symbols became more and more detached from their referents, the human brain had to recruit additional cortical resources to comprehend their meaning.

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References

1. Gombrich, E. *Art and Illusion: A study in the psychology of pictorial representation* (London: Phaidon Press, 1960).
2. Zeki S. 1999. *Inner vision: An exploration of art and the brain*. New York: Oxford University Press.
3. Mithen S. 1996. *The prehistory of the mind: A search for the origins of art, religion and science*. London: Thames and Hudson.
4. Vanhaerensy M, d'Errico F, Stringer C, James SL, Todd JA, Mienis HK. "Middle Paleolithic shell beads in Israel and Algeria." *Science* 312 (2006): 1785-1788.
5. Ede S. *Art & Science* (London, New York: I.B. Tauris, 2005).
6. Humphrey, N. "Cave art' autism, and the evolution of the human mind." *Cambridge Archeological Journal* 8 (1998): 165-191.
7. Jung-Beeman M, Bowden EM, Haberman J, Frymiare JL, Arambel-Liu S, Greenblatt R, Reber PJ, Kounios J. "Neural activity when people solve verbal problems with insight." *PLoS Biology* 2 (2004): 500-510.
8. Schneider P, Sluming V, Roberts N, Scherg M, Goebel R, Specht HJ, Dosch HG, Bleeck S, Stippich C, Rupp A. "Structural and functional asymmetry of lateral Heschl's gyrus reflects pitch perception preference." *Nature Neuroscience* 8 (2005): 1241-1247.
9. Stewart L. "Do musicians have different brains?" *Clinical Medicine* 8 (2008): 304-308.
10. Vogt S, Magnussen S. "Expertise in pictorial perception: eye-movement patterns and visual memory in artists and laymen." *Perception* 36 (2007): 91-100.
11. Solso RL. "Brain activities in a skilled versus a novice artist: an fMRI study." *Leonardo* 34 (2001): 31-34.
12. Thorpe S, Fize D, Marlot C. "Speed of processing in the human visual system." *Nature* 381 (1996): 520-522.
13. Biederman I. "Perceiving real-world scenes." *Science* 177 (1972): 77-80.
14. Bar M. "Visual objects in context." *Nature Review Neuroscience* 5 (2004): 617-629.
15. Ungerleider L.G., and Mishkin, M. "Two cortical visual systems." In: *Analysis of visual behavior*. D.J. Ingle, M.A. Goodale, R.J.W. Mansfield, eds. (Cambridge, MA: MIT Press, 1982).

16. Haxby JV, Horwitz B, Ungerleider LG, Maisog JM, Pietrini P, Grady CL. "The functional organization of human extrastriate cortex: a PET-rCBF study of selective attention to faces and locations." *Journal of Neuroscience* 14 (1994): 6336-6353.
17. Ishai A, Ungerleider LG, Martin A, Schouten JL, Haxby JV. "Distributed representation of objects in the human ventral visual pathway." *Proceedings National Academy of Sciences USA* 96 (1999): 9379-9384.
18. Ishai A, Ungerleider LG, Martin A, Haxby JV. "The representation of objects in the human occipital and temporal cortex." *Journal of Cognitive Neuroscience* 12 (2000): 35-51.
19. Haxby JV, Gobbini MI, Furey ML, Ishai A, Schouten JL, Pietrini P. "Distributed and Overlapping Representations of Faces and Objects In Ventral Temporal Cortex." *Science* 293 (2001): 2425-2430.
20. Kanwisher N, McDermott J, Chun MM. "The fusiform face area: A module in human extrastriate cortex specialized for face perception." *Journal of Neuroscience* 17 (1997): 4302-4311.
21. Aguirre, G.K., Zarahn, E., D'Esposito, M. "An area within human ventral cortex sensitive to "building" stimuli: Evidence and implications." *Neuron* 21 (1998): 1-20.
22. Chao LL, Haxby JV, Martin A. "Attribute-based neural substrates in posterior temporal cortex for perceiving and knowing about objects." *Nature Neuroscience* 2 (1999): 913-919.
23. Kleinschmidt A, Buchel C, Zeki S, Frackowiak RS. "Human brain activity during spontaneously reversing perception of ambiguous figures." *Proceedings of the Royal Society B: Biological Sciences* 265 (1998): 2427-2433.
24. Stanley DA, Rubin N. "fMRI activation in response to illusory contours and salient regions in the human lateral occipital complex." *Neuron* 37 (2003): 323-331.
25. Tong F, Nakayama K, Vaughan JT, Kanwisher N. "Binocular rivalry and visual awareness in human extrastriate cortex." *Neuron* 21 (1998): 753-759.
26. Roland, P.E., Eriksson, L., Stone-Elander, S., and Widen, L. 1987. Does mental activity change the oxidative metabolism of the brain? *Journal of Neuroscience* 7, 2373-2389.
27. Farah M, Peronnet F, Gonon MA, Giard MH. "Electrophysiological evidence for a shared representational medium for visual images and visual percepts." *Journal of Experimental Psychology: General* 117 (1988): 248-257.

28. Ishai A, Sagi D. "Common mechanisms of visual imagery and perception." *Science* 268 (1995): 1772-1774.
29. Ishai A, Sagi D. "Visual imagery facilitates visual perception: Psychophysical evidence." *Journal of Cognitive Neuroscience* 9 (1997): 476-489.
30. Ishai A, Sagi D. "Visual imagery: Effects of short- and long-term memory." *Journal of Cognitive Neuroscience* 9 (1997): 734-742.
31. Mellet E, Tzourio N, Crivello F, Joliot M, Denis M, Mazoyer B. "Functional anatomy of spatial mental imagery generated from verbal instructions." *Journal of Neuroscience* 16 (1996): 6504-6512.
32. Le Bihan D, Turner R, Zeffiro T, Cuendo C, Jezzard P, Bonnerot V. "Activation of human primary visual cortex during visual recall: A magnetic resonance imaging study." *Proceedings National Academy of Sciences USA* 90 (1993): 11802-11805.
33. Kosslyn SM, Alpert NM, Thompson WL, Maljkovic V, Weise SB, Chabris CF, Hamilton SE, Rauch SL, Buonanno FS. "Visual mental imagery activates topographically organized visual cortex: PET investigations." *Journal of Cognitive Neuroscience* 5 (1993): 263-287.
34. Levine DN, Warach J, Farah M. "Two visual systems in mental imagery: Dissociation of "what" and "where" in imagery disorders due to bilateral posterior cerebral lesions." *Neurology* 35 (1985): 1010-1018.
35. Amedi A, Malach R, Pascual-Leone A. "Negative BOLD differentiates visual imagery and perception." *Neuron* 48 (2005): 859-872.
36. Ishai A, Ungerleider LG, Haxby JV. "Distributed Neural Systems for the Generation of Visual Images." *Neuron* 28 (2000b): 979-990.
37. Miyashita Y, Chang HS. Neural correlate of pictorial short-term memory in the primate temporal cortex." *Nature* 331 (1988): 68-70.
38. Fletcher PC, Frith CD, Baker SC, Shallice T, Frackowiak RSJ, Dolan RJ. "The mind's eye - precuneus activation in memory-related imagery." *Neuroimage* 2 (1995): 195-200.
39. Buckner RL, Raichle ME, Miezin FM, Petersen SE. "Functional anatomic studies of memory retrieval for auditory words and visual pictures." *Journal of Neuroscience* 16 (1996): 6219-6235.
40. Mechelli A, Price CJ, Noppeney U, Friston KJ. "A Dynamic Causal Modeling Study on Category Effects: Bottom-Up or Top-Down Mediation?" *Journal of Cognitive Neuroscience* 15 (2003): 925-934.

41. Mechelli A, Price CJ, Friston KJ, Ishai A. "Where bottom-up meets top-down: neuronal interactions during perception and imagery." *Cerebral Cortex* 14 (2004): 1256-1265.
42. Haxby JV, Hoffman EA, Gobbini IM. "The distributed human neural system for face perception." *Trends in Cognitive Sciences* 4 (2000): 223-233.
43. Ishai A, Schmidt CF, Boesiger P. "Face perception is mediated by a distributed cortical network." *Brain Research Bulletin* 67 (2005): 87-93.
44. Ishai A, Yago E. "Recognition memory of newly learned faces." *Brain Research Bulletin* 71 (2006): 167-173.
45. Ishai A. "Let's face it: It's a cortical network." *NeuroImage* 40 (2008): 415-419.
46. Puce A, Allison T, Bentin S, Gore JC, McCarthy G, "Temporal Cortex Activation in Humans Viewing Eye and Mouth Movements." *Journal of Neuroscience* 18 (1998): 2188-2199.
47. Vuilleumier P, Armony JL, Driver J, Dolan RJ. "Effects of attention and emotion on face processing in the human brain: An event-related fMRI study." *Neuron* 30 (2001): 829-841.
48. Ishai A, Pessoa L, Bickle PC, Ungerleider LG. "Repetition Suppression of Faces is Modulated by Emotion." *Proceedings National Academy of Sciences USA* 101 (2004): 9827-9832.
49. Leveroni CL, Seidenberg M, Mayer AR, Mead LA, Binder JR, Rao SM. "Neural systems underlying the recognition of familiar and newly learned faces." *Journal of Neuroscience* 20 (2000): 878-886.
50. Aharon I, Etcoff N, Ariely D, Chabris CF, O'Connor E, Breiter HC. "Beautiful faces have variable reward value – fMRI and behavioral evidence." *Neuron* 32 (2001): 537-551.
51. O'Doherty J, Winston J, Critchley HD, Perrett D, Burt DM, Dolan RJ, "Beauty in a smile: the role of medial orbitofrontal cortex in facial attractiveness." *Neuropsychologia* 41 (2003): 147-155.
52. Kranz F, Ishai A. "Face perception is modulated by sexual preference." *Current Biology* 16 (2006): 63-68.
53. Ishai A. "Sex, beauty and the orbitofrontal cortex." *International Journal of Psychophysiology* 63 (2007): 181-185.

54. Fairhall, S.L., Ishai, A. "Effective connectivity within the distributed cortical network for face perception." *Cerebral Cortex* 17 (2007): 2400-2406.
55. Bar M, Aminoff E, Ishai A. "Famous faces activate contextual associations in the parahippocampal cortex." *Cerebral Cortex* 18 (2008): 1233-1238.
56. Ishai A, Haxby JV, Ungerleider LG. Visual Imagery of Famous Faces: Effects of Memory and Attention Revealed by fMRI. *NeuroImage* 17 (2002): 1729-1741.
57. Fairhall SL, Ishai A. "Neural correlates of object indeterminacy in art compositions." *Consciousness and Cognition* 17 (2008): 923-932.
58. Yago E, Ishai A. "Recognition memory is modulated by visual similarity." *Neuroimage* 31 (2006): 807-817.
59. Wiesmann M, Ishai A. Recollection- and familiarity-based memory decisions reflect memory strength. *Frontiers in Systems Neuroscience* 2 (2008): 1 (1-9). doi: 10.3389/neuro.06.001.2008
60. Gamberi D. *Potential Images: Ambiguity and indeterminacy in modern art* (London: Reaktion Books, 2002).
61. Pepperell R. "Seeing Without Objects: Visual Indeterminacy and Art." *Leonardo* 39 (2006): 394-400.
62. Ishai A, Fairhall SL, Pepperell R. "Perception, memory and aesthetics of indeterminate art." *Brain Research Bulletin* 73 (2007): 314-324.
63. Vartanian O, Goel V. "Neuroanatomical correlates of aesthetic preference for paintings." *Neuroreport* 15 (2004): 893-897.
64. Fink GR, Halligan PW, Marshall JC, Frith CD, Frackowiak RSJ, Dolan RJ. "Where in the brain does visual attention select the forest and the trees?" *Nature* 382 (1996): 626-628.
65. Corbetta M, Kincade MJ, Lewis C, Snyder AZ, Sapir A. "Neural basis and recovery of spatial attention deficits in spatial neglect." *Nature Neuroscience* 8 (2005): 1603-1610.
66. Kawabata H, Zeki S. "The neurology of beauty." *Journal of Neurophysiology* 91 (2004): 1699-1705.
67. Wiesmann M, Ishai A. "Training facilitates object recognition in Cubist paintings." *Frontiers in Human Neuroscience* 4 (2010): 11 (1-7). doi: 10.3389/neuro.09.011.2010

68. Epstein R, Kanwisher N. "A cortical representation of the local visual environment." *Nature* 392 (1998): 598-601.
69. Gabrieli JD, Brewer JB, Desmond JE, Glover GH. "Separate neural bases of two fundamental memory processes in the human medial temporal lobe." *Science* 276 (1997): 264-266.
70. Spiers HJ, Maguire EA. "The neuroscience of remote spatial memories: A tale of two cities." *Neuroscience* 149 (2007): 7-27.
71. Bar M. "The proactive brain: using analogies and associations to generate predictions." *Trends in Cognitive Sciences* 7 (2007): 280-289.
72. Kersten D, Mamassian P, Yuille A. "Object perception as Bayesian inference." *Annual Review of Psychology* 55 (2004): 271-304.
73. Friston KJ, Harrison L, Penny W. "Dynamic Causal Modeling." *NeuroImage* 19 (2003): 1273-1302.
74. Friston K. "A theory of cortical responses." *Philos Trans R Soc Lond B Biol Sci* 360 (2005): 815-836.
75. Fisher J. Entitling. *Critical Inquiry* 11 (1984): 286-298.
76. Leder H, Carbon CC, Ripsas AL. "Entitling art: Influence of title information on understanding and appreciation of paintings." *Acta Psychologica (Amst)* 121 (2006): 176-198.
77. Franklin MB, Becklen R, Doyle C. "The influence of titles on how paintings are seen." *Leonardo* 26 (1993): 103-108.
78. Kirk U, Skov M, Hulme O, Christensen MS, Zeki S. "Modulation of aesthetic value by semantic context: An fMRI study." *NeuroImage* 44 (2009): 1125-1132.