

V.S. Ramachandran and William Hirstein

The Science of Art

A Neurological Theory of Aesthetic Experience

We present a theory of human artistic experience and the neural mechanisms that mediate it. Any theory of art (or, indeed, any aspect of human nature) has to ideally have three components. (a) The logic of art: whether there are universal rules or principles; (b) The evolutionary rationale: why did these rules evolve and why do they have the form that they do; (c) What is the brain circuitry involved? Our paper begins with a quest for artistic universals and proposes a list of 'Eight laws of artistic experience' — a set of heuristics that artists either consciously or unconsciously deploy to optimally titillate the visual areas of the brain. One of these principles is a psychological phenomenon called the peak shift effect: If a rat is rewarded for discriminating a rectangle from a square, it will respond even more vigorously to a rectangle that is longer and skinnier than the prototype. We suggest that this principle explains not only caricatures, but many other aspects of art. Example: An evocative sketch of a female nude may be one which selectively accentuates those feminine form-attributes that allow one to discriminate it from a male figure; a Boucher, a Van Gogh, or a Monet may be a caricature in 'colour space' rather than form space. Even abstract art may employ 'supernormal' stimuli to excite form areas in the brain more strongly than natural stimuli. Second, we suggest that grouping is a very basic principle. The different extrastriate visual areas may have evolved specifically to extract correlations in different domains (e.g. form, depth, colour), and discovering and linking multiple features ('grouping') into unitary clusters — objects — is facilitated and reinforced by direct connections from these areas to limbic structures. In general, when object-like entities are partially discerned at any stage in the visual hierarchy, messages are sent back to earlier stages to alert them to certain locations or features in order to look for additional evidence for the object (and these processes may be facilitated by direct limbic activation). Finally, given constraints on allocation of attentional resources, art is most appealing if it produces heightened activity in a single dimension (e.g. through the peak shift principle or through grouping) rather than redundant activation of multiple modules. This idea may help explain the effectiveness of outline drawings and sketches, the savant syndrome in autists, and the sudden emergence of artistic talent in fronto-temporal dementia. In addition to these three basic principles we propose five others, constituting a total of 'eight laws of aesthetic experience' (analogous to the Buddha's eightfold path to wisdom).

Correspondence: V.S. Ramachandran, Center For Brain and Cognition, University of California, San Diego, La Jolla, CA 92093-0109, USA.

‘Everyone wants to understand art. Why not try to understand the song of a bird?’

Pablo Picasso

Introduction

If a Martian ethologist were to land on earth and watch us humans, he would be puzzled by many aspects of human nature, but surely art — our propensity to create and enjoy paintings and sculpture — would be among the most puzzling. What biological function could this mysterious behaviour possible serve? Cultural factors undoubtedly influence what kind of art a person enjoys — be it a Rembrandt, a Monet, a Rodin, a Picasso, a Chola bronze, a Moghul miniature, or a Ming Dynasty vase. But, even if beauty is largely in the eye of the beholder, might there be some sort of universal rule or ‘deep structure’, underlying all artistic experience? The details may vary from culture to culture and may be influenced by the way one is raised, but it doesn’t follow that there is no genetically specified mechanism — a common denominator underlying all types of art. We recently proposed such a mechanism (Ramachandran and Blakeslee, 1998), and we now present a more detailed version of this hypothesis and suggest some new experiments. These may be the very first experiments ever designed to empirically investigate the question of how the brain responds to art.

Many consider art to be a celebration of human individuality and to that extent it may seem like a travesty to even search for universals. Indeed theories of visual art range from curious anarchist views (or even worse, ‘anything goes’) to the idea that art provides the only antidote to the absurdity of our existence — the only escape, perhaps, from this vale of tears (Penrose, 1973). Our approach to art, in this essay, will be to begin by simply making a list of all those attributes of pictures that people generally find attractive. Notwithstanding the Dada movement, we can then ask, Is there a common pattern underlying these apparently dissimilar attributes, and if so, why is this pattern pleasing to us? What is the survival value, if any, of art?

But first let us clear up some common misconceptions about visual art. When the English colonizers first arrived in India they were offended by the erotic nudes in temples; the hips and breasts were grossly hypertrophied, the waist abnormally thin (Plate 1).¹ Similarly the Rajasthani and Moghul miniature paintings were considered primitive because they lacked perspective. In making this judgement they were, of course, unconsciously comparing Indian art with the ideals of Western representational art — Renaissance art in particular. What is odd about this criticism though, is that it misses the whole point of art. The purpose of art, surely, is not merely to depict or represent reality — for that can be accomplished very easily with a camera — but to enhance, transcend, or indeed even to *distort* reality. The word ‘*rasa*’ appears repeatedly in Indian art manuals and has no literal translation, but roughly it means ‘the very essence of.’ So a sculptor in India, for example, might try to portray the *rasa* of childhood (Plate 2), or the *rasa* of romantic love, or sexual ecstasy (Plate 3), or feminine grace and perfection (Plate 4). The artist is striving, in these images, to strongly evoke a direct emotional response of a specific kind. In Western art, the ‘discovery’ of non-representational abstract art had to await the arrival of Picasso. His nudes were also grotesquely distorted — both eyes on one side of the face for example. Yet when Picasso did it, the Western art critics heralded his attempts to

[1] Plates for the article can be downloaded free from www.imprint.co.uk/rama

‘transcend perspective’ as a profound new discovery — even though both Indian and African art had anticipated this style by several centuries!

We suggest in this essay that artists either consciously or unconsciously deploy certain rules or principles (we call them laws) to titillate the visual areas of the brain. Some of these laws, we believe, are original to this article — at least in the context of art. Others (such as grouping) have been known for a long time and can be found in any art manual, but the question of *why* a given principle should be effective is rarely raised: the principle is usually just presented as a rule-of-thumb. In this essay we try to present all (or many) of these laws together and provide a coherent biological framework, for only when they are all considered simultaneously and viewed in a biological context do they begin to make sense. There are in fact three cornerstones to our argument. First, what might loosely be called the ‘internal logic’ of the phenomenon (what we call ‘laws’ in this essay). Second, the evolutionary rationale: the question of *why* the laws evolved and have that particular form (e.g. grouping facilitates object perception). And third, the neurophysiology (e.g. grouping occurs in extrastriate areas and is facilitated by synchronization of spikes and direct limbic activation). All three of these need to be in place — and must inform each other — before we can claim to have ‘understood’ any complex manifestation of human nature — such as art. Many earlier discussions of art, in our view, suffer from the shortcoming that they view the problem from just one or two of these perspectives.

We should clarify at the outset that many aspects of art will not be discussed in this article — such as matters concerning style. Indeed it may well be that much of art really has to do with aggressive marketing and hype, and this inevitably introduces an element of arbitrariness that complicates the picture enormously. Furthermore the artistic ‘universals’ that we shall consider are not going to provide an instant formula for distinguishing ‘tacky’ or ‘tourist’ art, that hangs in the lobbies of business executives, from the genuine thing — even though a really gifted artist could do so instantly — and until we can do that we can hardly claim to have ‘understood’ art. Yet despite these reservations, we do believe that there is at least a component to art — however small — that IS lawful and can be analysed in accordance with the principles or laws outlined here. Although we initially proposed these ‘laws’ in a playful spirit, we were persuaded that there is enough merit in them to warrant publication in a philosophical journal. If the essay succeeds in stimulating a dialogue between artists, visual physiologists and evolutionary biologists, it will have adequately served its purpose.

The Essence of Art and the Peak Shift Principle

Hindu artists often speak of conveying the *rasa*, or ‘essence’, of something in order to evoke a specific mood in the observer. But what exactly does this mean? What does it mean to ‘capture the very essence’ of something in order to ‘evoke a direct emotional response’? The answer to these questions, it turns out, provides the key to understanding what art really is. Indeed, as we shall see, what the artist tries to do (either consciously or unconsciously) is to not only capture the essence of something but also to amplify it in order to more powerfully activate the same neural mechanisms that would be activated by the original object. As the physiologist Zeki (1998) has eloquently noted, it may not be a coincidence that the ability of the artist to abstract the ‘essential features’ of an image and discard redundant information is essentially identical to what the visual areas themselves have evolved to do.

Consider the *peak shift effect* — a well-known principle in animal discrimination learning. If a rat is taught to discriminate a square from a rectangle (of say, 3:2 aspect ratio) and rewarded for the rectangle, it will soon learn to respond more frequently to the rectangle. Paradoxically, however, the rat's response to a rectangle that is even longer and skinnier (say, of aspect ratio 4:1) is even greater than it was to the original prototype on which it was trained. This curious result implies that what the rat is learning is not a prototype but a rule, i.e. *rectangularity*. We shall argue in this essay that this principle holds the key for understanding the evocativeness of much of visual art. We are not arguing that it's the only principle, but that it is likely to be one of a small subset of such principles underlying artistic experience.

How does this principle — the peak shift effect — relate to human pattern recognition and aesthetic preference? Consider the way in which a skilled cartoonist produces a caricature of a famous face, say Nixon's. What he does (unconsciously) is to take the *average* of all faces, subtract the average from Nixon's face (to get the difference between Nixon's face and all others) and then *amplify* the differences to produce a caricature. The final result, of course, is a drawing that is even more Nixon-like than the original. The artist has amplified the differences that characterize Nixon's face in the same way that an even skinnier rectangle is an amplified version of the original prototype that the rat is exposed to. This leads us to our first aphorism: 'All art is caricature'. (This is not *literally* true, of course, but as we shall see, it is true surprisingly often.) And the same principle that applies for recognizing faces applies to all aspects of form recognition. It might seem a bit strange to regard caricatures as art but take a second look at the Chola bronze — the accentuated hips and bust of the Goddess Parvati (Plate 1) and you will see at once that what you have here is essentially a caricature of the female form. There may be neurons in the brain that represent sensuous, rotund feminine form as opposed to angular masculine form and the artist has chosen to amplify the 'very essence' (the *rasa*) of being feminine by moving the image even further along toward the feminine end of the female/male spectrum (Plate 4). The result of these amplifications is a 'super stimulus' in the domain of male/female differences. It is interesting, in this regard, that the earliest known forms of art are often caricatures of one sort or another; e.g. prehistoric cave art depicting animals like bison and mammoths, or the famous Venus 'fertility' figures.

As a further example, look at the pair of nudes in Plate 5, a sculpture from Northern India (circa 800 AD). No normal woman can adopt such contorted postures and yet the sculpture is incredibly evocative — beautiful — capturing the *rasa* of feminine poise and grace. To explain how he achieves this effect, consider the fact that certain postures are impossible (and unlikely) among men but possible in women because of certain anatomical differences that impose constraints on what can or cannot be done. Now in our view what the artist has done here is to subtract the male posture from the female posture to produce a caricature in 'posture space' thereby amplifying 'feminine posture' and producing a correspondingly high limbic activation. The same can be said of the dancer in Plate 6 or for the amorous couple (Plate 7). Again, even though these particular, highly stylized anatomical poses are impossible (or unlikely) it is very evocative of the 'Srīngara Rasa' or 'Kama rasa' (sexual and amorous ecstasy) because the artist is providing a 'caricature' that exaggerates the amorous pose. It is as though the artist was able to intuitively access and powerfully stimulate neural mechanisms in the brain that represent 'amorousness'.

A *posture space* might be realized in the form of a large set of remembered postures of people one has observed. (Whether one might expect such a memory mapping to exist in the ‘dorsal’ stream of visual processing, which connects with the agent’s own body representations, or the ‘ventral’ stream, known to be used for face perception, is an interesting question; perhaps the answer is, both). There is an obvious need to connect these posture representations to the limbic system: it is quite imperative that I recognize an attack posture, a posture — or body position — which beckons me, or one which indicates sadness or depression, etc. The sculptors of Plates 5 and 6 relied on this represented posture space in creating their works. The sculptor knows, consciously or not, that the sight of those postures will evoke a certain sort of limbic activation when the posture is successfully represented in the posture space system — he tells a story in this medium, we might say.

Until now we have considered caricatures in the form domain, but we know from the pioneering work of many physiologists (Zeki, 1980; see also Livingstone and Hubel, 1987; Allman & Kaas, 1971; Van Essen & Maunsell, 1980) that the primate brain has specialized modules concerned with other visual modalities such as colour depth and motion. Perhaps the artist can generate caricatures by exploiting the peak shift effect along dimensions other than form space, e.g., in ‘colour space’ or ‘motion space’. For instance consider the striking examples of the plump, cherub-faced nudes that Boucher is so famous for. Apart from emphasizing feminine, neotonous baby-like features (a peak shift in the masculine/feminine facial features domain) notice how the skin tones are exaggerated to produce an unrealistic and absurd ‘healthy’ pink flush. In doing this, one could argue he is producing a *caricature in colour space*, particularly the colours pertaining to male/female differences in skin *tone*. Another artist, Robert, on the other hand, pays little attention to colour or even to form, but tends to deliberately overemphasize the textural attributes of his objects, be they bricks, leaves, soil, or cloth. And other artists have deliberately exaggerated (‘caricatured’ or produced peak shifts in) shading, highlights, illumination etc to an extent that would never occur in a real image. Even music may involve generating peak shifts in certain primitive, passionate primate vocalizations such as a separation cry; the emotional response to such sounds may be partially hard-wired in our brains.

A potential objection to this scheme is that it is not always obvious in a given picture what the artist is trying to caricature, but this is not an insurmountable objection. Ethologists have long known that a seagull chick will beg for food by pecking at its mother’s beak. Remarkably, it will peck just as vigorously at a disembodied beak with no mother attached or even a brown stick with a red dot at the end (the gull’s beak has a vivid red spot near the tip). The stick with the red dot is an example of a ‘releasing stimulus’ or ‘trigger feature’ since, as far as the chick’s visual system is concerned this stimulus is as good as the entire mother bird. What is even more remarkable, though, was Tinbergen’s discovery (Tinbergen, 1954) that a very long, thin brown stick, with *three* red stripes at the end is even more effective in eliciting pecks than the original beak, even though it looks nothing like a beak to a human observer.

The gull’s form recognition areas are obviously wired-up in such a way that Tinbergen had inadvertently produced a super stimulus, or a caricature in ‘beak space’ (e.g. the neurons in the gull’s brain might embody the rule ‘more red contour the better’). Indeed, if there were an art gallery in the world of the seagull, this ‘super beak’ would qualify as a great work of art — a Picasso. Likewise, it is possible that some types of

art such as cubism are activating brain mechanisms in such a way as to tap into or even caricature certain innate form primitives which we do not yet fully understand.² At present we have no idea what the ‘form primitives’ used by the human visual pathways are, but we suggest that many artists may be unconsciously producing heightened activity in the ‘form areas’ in a manner that is not obvious to the conscious mind, just as it isn’t obvious why a long stick with *three* red stripes is a ‘super beak’. Even the sunflowers of Van Gogh or the water lilies of Monet may be the equivalent — in colour space — of the stick with the three stripes, in that they excite the visual neurons that represent colour memories of those flowers even more effectively than a real sunflower or water lily might.

There is also clearly a mnemonic component of aesthetic perception, including, the autobiographical memory of the artist, and of her viewer, as well as the viewer’s more general ‘cognitive stock’ brought to his encounter with the work. This general cognitive stock includes the viewer’s memory of his encounters with the painting’s etiological forebears, including those works that the artist himself was aware of. Often paintings contain homages to earlier artists and this concept of homage fits what we have said about caricature: the later artist makes a caricature of his acknowledged predecessor, but a loving one, rather than the ridiculing practised by the editorial cartoonist. Perhaps some movements in the history of art can be understood as driven by a logic of peak shift: the new art form finds and amplifies the essence of a previous one (sometimes many years previous, in the case of Picasso and African art).³

- [2] Another manifestation of this principle can be seen in the florid sexual displays of birds — that we find so attractive. It is very likely, as suggested by Darwin, that the grotesque exaggeration of these displays, for example the magnificent wings of the birds of paradise, is a manifestation of the peak shift effect during mate choice — sexual selection caused by birds of each generation preferring caricatures of the opposite sex to mate with (just as humans lean toward Playboy pinups and Chippendale dancers). Indeed we have recently suggested (Ramachandran and Blakeslee, 1998) that many aspect of morphological evolution (not just ‘secondary sexual characteristics’ or florid ‘ethological releasers’ and threat displays) may be the outcome of runaway selection, based on the peak shift principle. The result would be not only the emergence and ‘quantization’ of new species, but also a progressive and almost comical ‘caricaturization’ of phylogenetic trends of precisely the kind one sees in the evolution of elephants or ankylosaurs. Even the quirks of fashion design (e.g. corsets becoming absurdly narrow, shoes becoming smaller and smaller in ancient China, shrinking miniskirts) become more comprehensible in terms of this perceptual principle. One wonders, also, whether the striking resemblance between the accumulation of jewellery, shoes and other brightly coloured objects by humans and the collections of bright pebbles, berries and feathers by bowerbirds building their enormous nests is entirely coincidental.
- [3] Lastly, consider the evolution of facial expressions. Darwin proposed that a ‘threat gesture’ may have evolved from the real facial movements one makes before attacking a victim — i.e. the baring of canines, etc. The same movement may eventually become divorced from the actual act and begin to serve as a *communication of intent* — a threat. If the peak shift principle were to operate in the recipient’s brain it is easy to see how such a ritualized signal would become progressively amplified across generations. Darwin had a difficult time, however, explaining why gestures such as sadness (instead of joy) seem to involve the opposite movement of facial features — e.g. lowering the corners of the mouth — and he came up with his somewhat *ad hoc* ‘principle of antithesis’, which states that somehow the opposite emotion is automatically linked to the opposite facial movements. We would suggest, instead, that the principle of antithesis is, once again, an indirect result of the recipient’s brain applying the peak shift principle. Once the organism has circuitry in its brain that says K is normal and J is a smile, then it may follow automatically that L is the expression of the opposite emotion — sadness. Whether this particular conjecture is correct or not we believe that emotional expressions analysed in terms of the peak shift effect may begin to make more sense than they have in the past.

Another layer of complexity here is that even the *perception* of complex postures or actions may



Figure 1
A jumble of splotches or a face?
[If you have difficulty 'seeing' the face, try looking through half-closed eyes — Editor.]



Figure 2
Initially seen as a jumble of splotches, once the Dalmatian is seen, its spots are grouped together — a pleasing effect, caused perhaps by activation of the limbic system by temporal lobe cortex.

Perceptual Grouping and Binding is Directly Reinforcing

One of the main functions of 'early vision' (mediated by the thirty or so extrastriate visual areas) is to discover and delineate *objects* in the visual field (Marr, 1981; Ramachandran, 1990; Pinker, 1998; Shepard, 1981) and for doing this the visual areas rely, once again, on extracting correlations. For instance if a set of randomly placed spots A is superimposed on another set of randomly placed dots B, they are seen to mingle to form just a single enormous cluster. But if you now *move* one of the clusters (say, A) then all the dots are instantly glued or bound together perceptually to create an object that is clearly separate from the background cluster B. Similarly if cluster A is made of red dots (and B is of green dots) we have no difficulty in segregating them instantly.

This brings us to our second point. The very process of discovering correlations and of 'binding' correlated features to create unitary objects or events must be *reinforcing* for the organism — in order to provide incentive for discovering such correlations (Ramachandran and Blakeslee, 1998). Consider the famous hidden face (Fig. 1)

require the observer to somehow internally re-enact or 'rehearse' the action before it is identified. For instance, patients with apraxia (inability to perform complex skilled movements resulting from damage to the left supramarginal gyrus) often, paradoxically, have difficulty perceiving and recognizing complex actions performed by others. Also, there are cells in the frontal lobes thought to be involved in the production of complex movements but which also fire when the animal perceives the same movements performed by a the experimenter (di Pellegrino *et al.*, 1992). This finding — together with the peak shift effect — would help account for Darwin's 'principle of antithesis', which would otherwise seem completely mysterious. Such cells may also be activated powerfully when viewing dynamic figural representations such as the 'Dancing Devi' (Plate 6).

or Dalmatian dog photo (Fig. 2). This is seen initially as a random jumble of splotches. The number of potential groupings of these splotches is infinite but once the dog is seen your visual system links only a subset of these splotches together and it is impossible *not* to ‘hold on’ to this group of linked splotches. Indeed the discovery of the dog and the linking of the dog-relevant splotches generates a pleasant ‘aha’ sensation. In ‘colour space’ the equivalent of this would be wearing a blue scarf with red flowers if you are wearing a red skirt; the perceptual grouping of the red flowers and your red skirt is aesthetically pleasing — as any fashion designer will tell you. These examples suggest that there may be direct links in the brain between the processes that discover such correlations and the limbic areas which give rise to the pleasurable ‘rewarding’ sensations associated with ‘feature binding’. So when you choose a blue mat to frame your painting in order to ‘pick up’ flecks of blue in the painting you are indirectly tapping into these mechanisms.

How is such grouping achieved? As noted above, the primate brain has over two dozen visual areas each of which is concerned with a different visual attribute such as motion, colour, depth, form, etc. These areas are probably concerned with extracting correlations in ‘higher dimensional’ spaces — such as ‘colour space’ or ‘motion space’. In a regular topographic map — e.g., in area 17 — features that are close together in physical space are also close together in the brain (which is all that is meant by ‘map’). But now think of *non-topographic* maps — say a map of ‘colour space’ — in which points that are close together in *wavelength* are mapped close together in the colour area of the brain *even though they may be distant from each other physically* (Barlow, 1986). Such proximity along different feature dimensions may be useful for perceptual grouping and ‘binding’ of features that are similar within that dimension.

This argument sounds plausible, but why should the outputs of separate vision modules — space, colour, depth, motion, etc. — be sent *directly* to the limbic system before further processing has occurred? Why not delay the reinforcement produced by limbic activation until the object has actually been identified by neurons in infero-temporal cortex? After all, the various Gestalt grouping processes are thought to occur autonomously as a result of computations within each module itself (Marr, 1981) without benefit of either cross-module or ‘top down’ influences — so why bother hooking up the separate modules themselves to limbic regions? One resolution of this paradox might simply be that the serial, hierarchical, ‘bucket brigade’ model of vision is seriously flawed and that eliminating ambiguity, segmenting the scene and discovering and identifying objects do indeed rely on top down processes — at least to some situations (Churchland *et al.*, 1994). The visual system is often called upon to segment the scene, delineate figure from ground and recognize objects in very noisy environments — i.e., to defeat camouflage — and this might be easier to accomplish if a limbic ‘reinforcement’ signal is not only fed back to early vision once an object has been completely identified, but is evoked at each and every stage in processing as soon as a partial ‘consistency’ and binding is achieved. This would explain why we say ‘aha’ when the Dalmatian is finally seen in Fig. 2 — and why it is difficult to revert back to seeing merely splotches once the dog is seen as a whole: that particular percept is powerfully reinforced (Ramachandran and Blakeslee, 1998). In other words, even though the grouping may be initially based on autonomous process in each module (Marr, 1981), once a cluster of features becomes perceptually salient

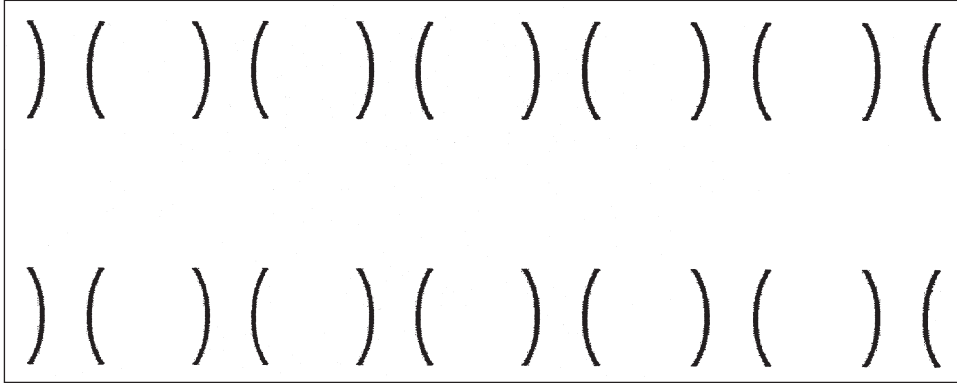


Figure 3

Gestalt grouping principles. The tokens can be grouped either on the basis of ‘proximity’ (which produces hourglasses), or ‘closure’. The latter organization is more stable and pleasing to the eye.

as a ‘chunk’ with boundaries (i.e. an object), it may send a signal to the limbic centres which in turn causes you to ‘hold on’ to that chunk to facilitate further computation. There is physiological evidence that grouping of features leads to synchronization of the spikes (action potentials) of neurons that extract those features (Singer and Gray, 1995; Crick and Koch, 1998) and perhaps it is this synchrony that allows the signal to be sent to the limbic pathways. (This, by the way, may be one reason why musical consonance often involves harmonics — for example, a C-major chord — which, for physical reasons would tend to emerge from a single object, whereas dissonant notes are likely to emerge from two or more separate objects.)

The key idea, then, is the following (and it applies to many of our laws, not just grouping). Given the limited attentional resources in the brain and limited neural space for competing representations, at *every* stage in processing there is generated a ‘Look here, there is a clue to something potentially object-like’ signal that produces limbic activation and draws your attention to that region (or feature), thereby facilitating the processing of those regions or features at earlier stages. Furthermore, partial ‘solutions’ or conjectures to perceptual problems are fed back from every level in the hierarchy to every earlier module to impose a small bias in processing and the final percept emerges from such progressive ‘bootstrapping’ (Ramachandran *et al.*, 1998). As noted above, consistency between partial high-level ‘hypotheses’ and earlier low-level ensembles also generates a pleasant sensation — e.g. the Dalmatian dog ‘hypothesis’ encourages the binding of corresponding splotches which, in turn, further consolidate the ‘dog-like’ nature of the final percept and we feel good when it all finally clicks in place. And what the artist tries to do, is to tease the system with as many of these ‘potential object’ clues as possible — an idea that would help explain why grouping and ‘perceptual problem solving (see below) are both frequently exploited by artists and fashion designers.

The notion that art exploits grouping principles is of course not new (Gombrich, 1973; Arnheim, 1956; Penrose, 1973), but what is novel here is our claim that the grouping doesn’t always occur ‘spontaneously’; that out of a temporary binding a signal sent to the limbic system to reinforce the binding, and this is one source of the aesthetic experience. For example, in Fig. 3, there are two possible stable organiza-

tions, one with hourglasses, and one with closure and most people find the latter organization more pleasing than the former because the limbic activation is stronger with this closure-based object-like percept. When artists speak of composition, or grouping, they are probably unconsciously tapping into these very same principles. One obvious prediction that emerges from this theory is that patients with Kluver-Bucy syndrome — caused by bilateral amygdala destruction — should not only display problems in recognizing objects (visual agnosia) but also in segmenting them out from noisy backgrounds, an idea that would be relatively easy to test experimentally.

Isolating a Single Module and Allocating Attention

The third important principle (in addition to peak shift and binding) is the need to *isolate* a single visual modality before you amplify the signal in that modality. For instance, this is why an outline drawing or sketch is more effective as ‘art’ than a full colour photograph. This seems initially counterintuitive since one would expect that the richer the cues available in the object the stronger the recognition signal and associated limbic activation. This apparent objection can be overcome, however, once one realizes that there are obvious constraints on the *allocation of attentional resources* to different visual modules. Isolating a single area (such as ‘form’ or ‘depth’ in the case of caricature or Indian art) allows one to direct attention more effectively to this one source of information, thereby allowing you to notice the ‘enhancements’ introduced by the artist. (And that in turn would amplify the limbic activation and reinforcement produced by those enhancements). Consider a full-colour illustration of Nixon, with depth, shading, skin tones and blemishes, etc. What is unique about Nixon is the form of his face (as amplified by the caricature) but the skin tone — even though it makes the picture more human-like — doesn’t contribute to making him ‘Nixon like’ and therefore actually detracts from the efficacy of the form cues. Consequently, one would predict that a full colour photo of Nixon would actually be *less* aesthetically pleasing than a sketchy outline drawing that captures the essential ‘Nixon-like’ attributes of his face.

The idea that outlines are effective in art is hardly new. It has been repeated *ad nauseum* by many authors, ever since David Hubel and Torsten Wiesel (1979) originally pointed out that this principle may reflect the fact that cells in the visual pathways are adequately stimulated by edges and are indifferent to homogeneous regions. However this would only explain why one can *get away* with just using outlines — not why outlines are actually *more* effective than a full colour half tone photo, which, after all, has more information. We would argue that when the colour, skin texture, etc. are not critical for defining the identity of the object in question (e.g. Nixon’s face) then the extra redundant information can actually distract your limited attentional resources away from the defining attributes of that object. Hence the aphorism ‘more is less’ in Art.⁴

Additional evidence for this view comes from the ‘savant syndrome’ — autistic children who are ‘retarded’ and yet produce beautiful drawings. The animal drawings of the eight-year old artist Nadia, for instance, are almost as aesthetically pleasing as

[4] If this theory is correct, we can make the counterintuitive prediction that activation of the face area in the brain — measured by fMRI — should, paradoxically, be greater for an outline sketch of a face than for a full colour photo of a face.

those of Leonardo da Vinci! (Plate 8). We would argue that this is because the fundamental disorder in autism is a distortion of the ‘saliency landscape’; they shut out many important sensory channels thereby allowing them to deploy all their attentional resources on a single channel; e.g., in ‘visual form representation’ channel in the case of Nadia. This idea is also consistent with the ingenious theory of Snyder (Snyder and Thomas, 1997), that savants are able to ‘directly access’ the outputs of some of their early vision modules because they are less ‘concept driven’: the conceptual impoverishment that produces autism also, paradoxically, gives them better access to earlier processes in vision. And finally, we would suggest that the ‘isolation’ principle also explains the efflorescence of artistic talent that is occasionally seen in fronto-temporal dementia in adults: a clinical phenomenon that is currently being studied intensively in our laboratory.

These ideas allow us to make certain novel predictions: If you put luminous dots on a person’s joints and film him or her walking in complete darkness, the complex motion trajectories of the dots are usually sufficient to evoke a compelling impression of a walking person — the so-called Johansson effect (Johansson, 1975). Indeed, it is often possible to tell the sex of the person by watching the gait. However, although these movies are often comical, they are not necessarily pleasing aesthetically. We would argue that this is because even though you have isolated a cue along a single dimension, i.e., motion, this isn’t really a caricature in motion space. To produce a work of art, you would need to subtract the female motion trajectories from the male and amplify the difference. Whether this would result in a pleasing work of kinetic art remains to be seen.

Contrast Extraction is Reinforcing

Grouping, as we have already noted, is an important principle, but the extraction of features prior to grouping — which involves discarding redundant information and extracting *contrast* — is also ‘reinforcing’. Cells in the retina, lateral geniculate body (a relay station in the brain) and in the visual cortex respond mainly to edges (step changes in luminance) but not to homogeneous surface colours; so a line drawing or cartoon stimulates these cells as effectively as a ‘half tone’ photograph. What is frequently overlooked though is that such contrast extractions — as with grouping — may be intrinsically pleasing to the eye (hence the efficacy of line drawings). Again, though, if contrast is extracted autonomously by cells in the very earliest stages of processing, why should the process be rewarding in itself? We suggest that the answer once again has to do with the allocation of *attention*. Information (in the Shannon sense) exists mainly in regions of change — e.g. edges — and it makes sense that such regions would, therefore, be more attention grabbing — more ‘interesting’ — than homogeneous areas. So it may not be coincidental that what the cells find interesting is also what the organism as a whole finds interesting and perhaps in some circumstances ‘interesting’ translates into ‘pleasing’.

For the same reason, contrast along many other stimulus dimensions besides luminance, such as colour or texture, has been exploited by artists (for instance, colour contrast is exploited by Matisse), and indeed there are cells in the different visual areas specialized for colour contrast, or motion contrast (Allman and Kaas, 1971). Furthermore, just as one can speak of a peak shift principle along very abstract dimen-

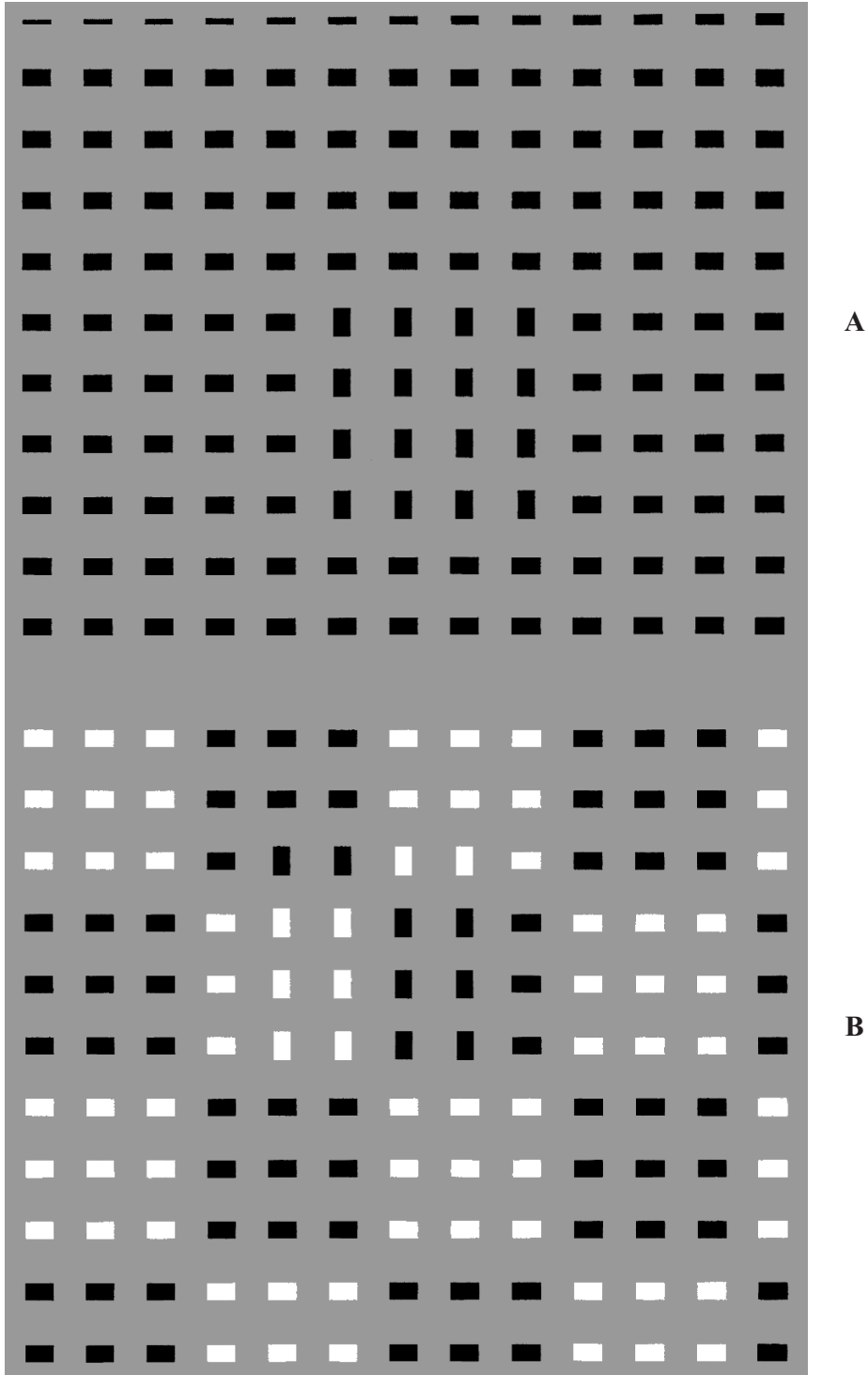


Figure 4
 Camouflage. Notice that the boundary between the two types of texture (vertical vs. horizontal lines) is clearly visible on the upper pattern (A), but is masked by the luminance boundaries on the lower (B). (Based on M.J. Morgan; personal communication).

sions, contrast can also emerge in dimensions other than luminance or colour. For instance, a nude wearing baroque (antique) gold jewellery (and nothing else) is aesthetically much more pleasing than a completely nude woman or one wearing both jewellery and clothes, presumably because the homogeneity and smoothness of the naked skin contrasts sharply with the ornateness and rich texture of the jewellery. Whether the analogy between luminance contrast extracted by cells in the brain and the contrast between jewels and naked skin is just a play of words or a deep unifying principle is a question that cannot be answered given what we know about the brain. But we do know that the attention grabbing effect of contrast must be a very important principle in nature, since it is often used as a camouflage device by both predators and their prey. For instance, in Fig. 4A, a texture border is very visible, but in Fig. 4B it is almost 'invisible', camouflaged by the colour (black/white) borders that grab the lion's share of your attention.

At first the two principles we have just considered seem antithetical; grouping on the basis of similarity is rewarding, but if so how can contrast (the very opposite of grouping) also be rewarding? One clue comes from the fact that the two mechanisms have different spatial constraints; grouping can occur between similar features (e.g. colour or motion) even if they are far apart in space (e.g., the spots on the nose and tail of a leopard). Contrast, on the other hand, usually occurs between dissimilar features that are physically close together. Thus even though the two processes seem to be inconsistent, they actually complement one another in that they are both concerned with the discovery of objects — which is the main goal of vision. (Contrast extraction is concerned with the object's boundaries whereas grouping allows recovery of the object's surfaces and, indirectly, of its boundaries as well). It is easy to see then why the two should be mutually reinforcing and rewarding to the organism.

Symmetry

Symmetry, of course, is also aesthetically pleasing as is well known to any Islamic artist (or indeed to any child looking through a kaleidoscope) and it is thought to be extracted very early in visual processing (Julesz, 1971). Since most biologically important objects — such as predator, prey or mate are symmetrical, it may serve as an early-warning system to grab our attention to facilitate further processing of the symmetrical entity until it is fully recognised. As such, this principle complements the other laws described in this essay; it is geared towards discovering 'interesting' object-like entities in the world.

Intriguingly, it has recently been shown experimentally that when choosing a mate, animals and humans prefer symmetrical over asymmetrical ones and evolutionary biologists have argued that this is because parasitic infestation — detrimental to fertility — often produces lopsided, asymmetrical growth and development. If so, it is hardly surprising that we have a built-in aesthetic preference for symmetry.

The Generic Viewpoint and the Bayesian Logic of Perception

Another less well known principle relates to what AI researchers refer to as 'the generic viewpoint' principle, which is illustrated in Fig. 5A and B and Fig. 6A and B. In Fig. 5A most people see a square occluding the corner of another square, even

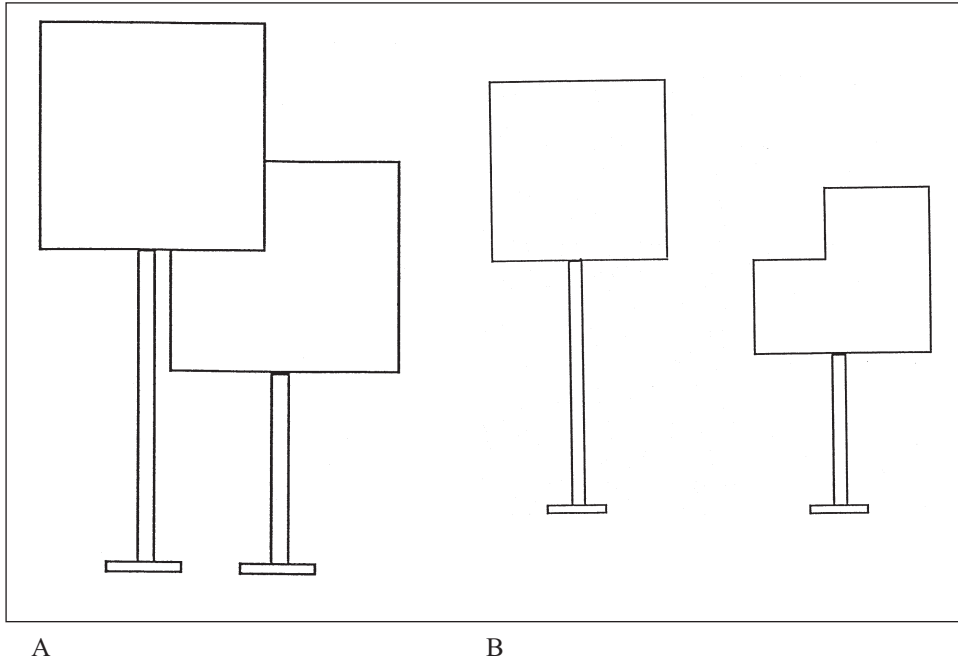


Figure 5

One square is seen as occluding the other. It is hard to see A as B viewed from a unique vantage point. The brain 'prefers' the generic view.

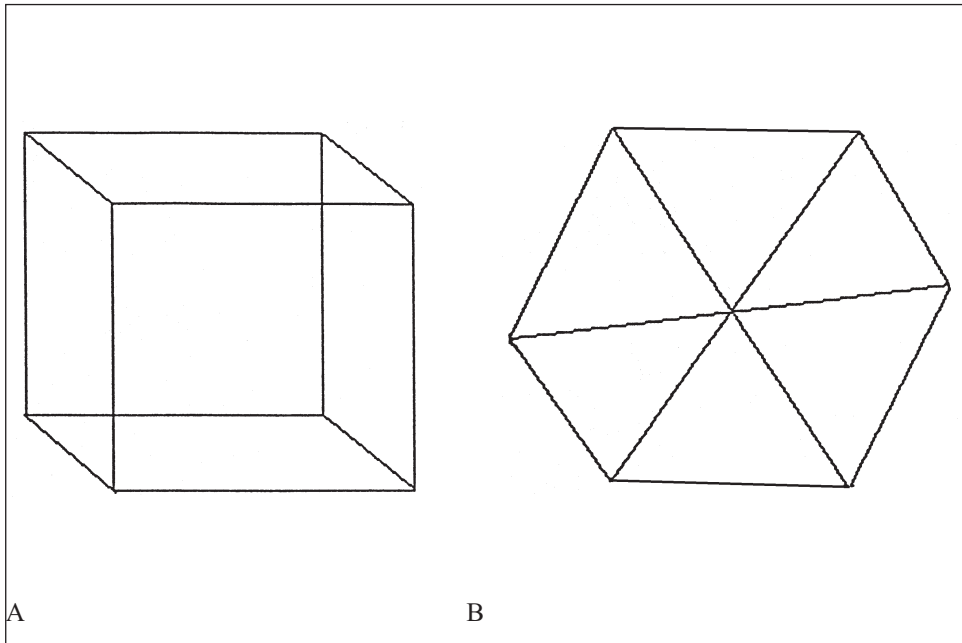


Figure 6

The flat hexagon with radiating spokes could be a cube but is never seen as one. The 'generic' interpretation is again the brain's preferred one.

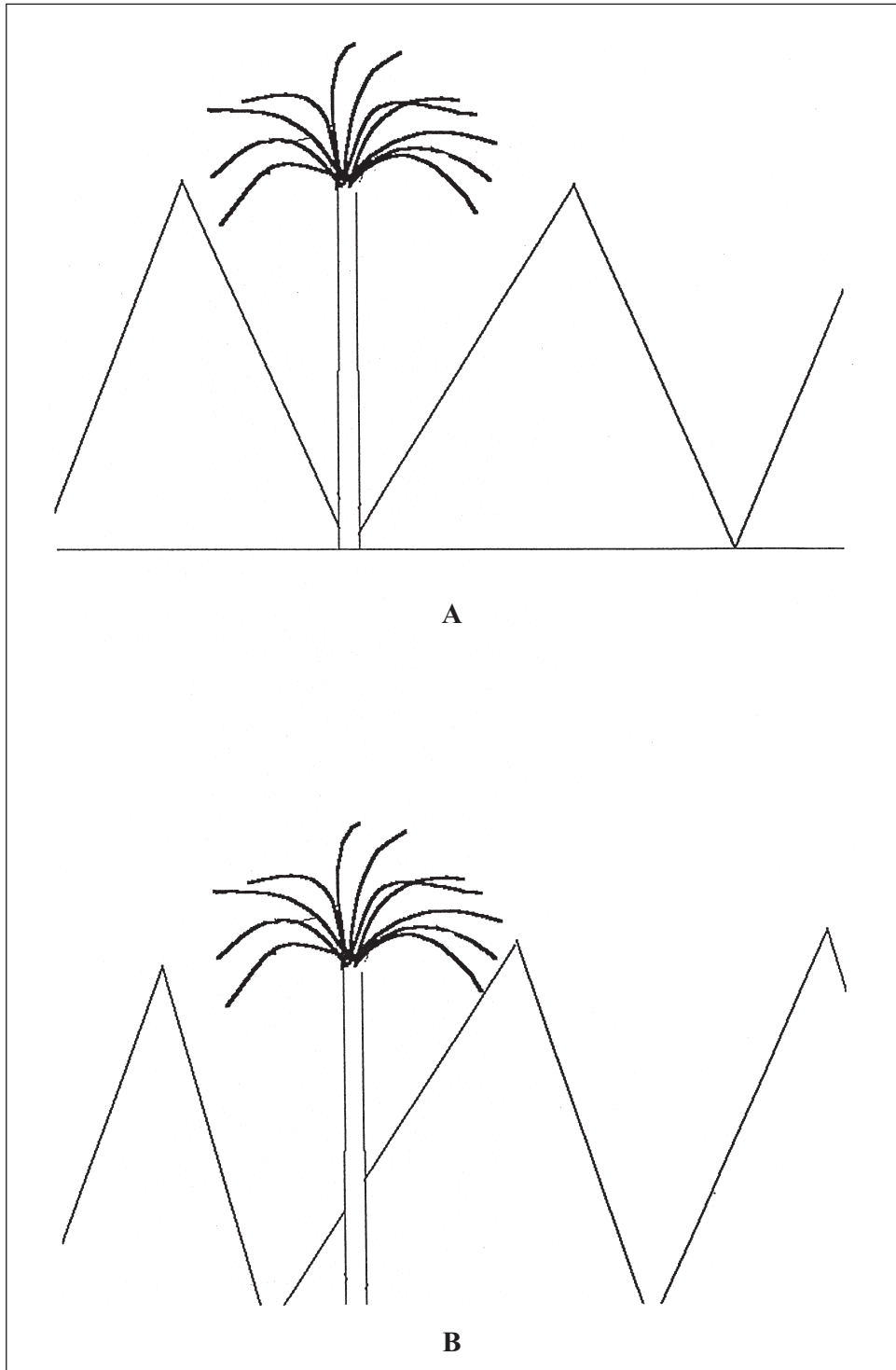


Figure 7

The brain's abhorrence of 'suspicious coincidences' (a phrase used by Horace Barlow). Figure B is pleasing, but A is distasteful to the eye.

though it could theoretically be Fig. B seen from a unique view point. The reason is that there is an infinite set of viewpoints that could produce the class of retinal images resembling A, but only a single, unique viewpoint that could produce retinal image A, given the objects in B. Consequently, the visual system rejects the latter interpretation as being highly improbable and prefers to see A as occlusion. (The same principle applies to 6A and B; A could depict an outline of a cube seen from one specific vantage point, but people usually see it as a flat hexagon with spokes radiating from the middle.) These examples illustrate the universal Bayesian logic of all perception: your visual system abhors interpretations which rely on a unique vantage point and favours a generic one or, more generally, it abhors suspicious coincidences (Barlow, 1980). For this reason, Fig. 7B is pleasing, whereas 7A is unattractive (palm tree and hills). So if an artist is trying to please the eye, he too, should avoid coincidences, such as those in 7A and 6B. Yet one must be cautious in saying this since every now and then — given the perverse nature of art and artists — a pleasing effect can be produced by *violating* this principle rather than adhering to it. For instance, there is a Picasso nude in which the *improbability* of the arm's outline exactly coinciding with that of the torso grabs the viewer's attention — and is arguably attractive to him!

We hasten to add that the principles we have discussed so far certainly do not exhaust all types of artistic experience. We have hardly touched on the purely symbolic or allegorical aspects of some types of paintings or sculpture, or on surrealism and modern abstract art (e.g., minimalists such as Kandinsky), not to mention 'counter' art such as the Dada movement. Also very puzzling is the question of why a nude hidden by a diaphanous veil is more alluring than one seen directly in the flesh, as pointed out by Ernst Gombrich (1973). It is as though an object discovered after a struggle is more pleasing than one that is instantly obvious. The reason for this is obscure but perhaps a mechanism of this kind ensures that the struggle *itself* is reinforcing — so that you don't give up too easily — whether looking for a leopard behind foliage or a mate hidden in the mist. On the other hand, we suspect that surrealist art really doesn't have much to do with visual representations *per se* but involves playing with links between vision and semantics, thereby taking it closer to the metaphorical ambiguities of poetry and language than to the purely visual appeal of a Picasso, a Rodin, or a Chola bronze. For example, in his erotic masterpiece 'Young virgin autosodomised by her own chastity' (1954), Dali has used the male penis to represent the female buttocks and genitalia. The medium and message 'resonate' since they both pertain to sex but they are also in subtle conflict since they depict 'opposite' sexes! The result is an image pleasing on many levels simultaneously. This playful, whimsical, aspect of art, often involving the humorous juxtaposition of complementary — or sometimes even incongruous — elements, is perhaps the most enigmatic aspect of our aesthetic experience, one which we have hardly touched upon in this essay. Another aspect of art that we have not dealt with is *style*, although one can see how once a style or trend is set in motion the peak shift principle can certainly help amplify it.

Art as Metaphor

The use of visual metaphors in art is well known. For instance, in Plate 9, the languorous, sensuous pose of the woman mimics the tree branch above — the curves match her curves and perhaps the tree's fertility is a metaphor for her youthfulness. (Just as

in Plate 4, the fruit in the tree echoes the curve of the breasts as well as the abdomen.) There are countless examples of this sort in both Eastern and Western art and yet the question is rarely raised as to *why* visual ‘puns’ or allegories should be aesthetically pleasing. A metaphor is a mental tunnel between two concepts or percepts that appear grossly dissimilar on the surface. When Shakespeare says ‘Juliet is the sun,’ he is appealing to the fact that they are both warm and nurturing (not the fact that they both reside in our solar system!). But, again, why should grasping an analogy of this kind be so rewarding to us? Perhaps the use of a simple concrete example (or one that is easily visualised, such as the sun) allows us to ignore irrelevant, potentially distracting aspects of an idea or percept (e.g. Juliet has nails, teeth and legs) and enables us to ‘highlight’ the crucial aspects (radiance and warmth) that she shares with the sun but not with other women. Whether this is purely a device for effective communication, or a basic cognitive mechanism for encoding the world more economically, remains to be seen. The latter hypothesis may well be correct. There are many paintings that instantly evoke an emotional response long before the metaphor is made explicit by an art critic. This suggests that the metaphor is effective even before one is conscious of it, implying that it might be a basic principle for achieving economy of coding rather than a rhetorical device. This is also true of poetic metaphors, as when Shakespeare says of Juliet, ‘Death, that has sucked the honey of thy breath’: the phrase is incredibly powerful well before one becomes consciously aware of the hidden analogy between the ‘sting of death’ and the bee’s sting and the subtle sexual connotations of ‘sucking’ and ‘breath’.

Classifying objects into categories is obviously vital for survival, e.g. prey vs. predator, edible vs. inedible, male vs. female, etc. Seeing a deep similarity — a common denominator as it were — between disparate entities is the basis of all concept formation whether the concepts are perceptual (‘Juliet’) or more abstract (‘love’). Philosophers often make a distinction between categories or ‘types’ and ‘tokens’ — the exemplars of a type — (e.g. ‘ducks’ vs. ‘that duck’). Being able to transcend tokens to create types is an essential step in setting up a new perceptual category. Being able to see the hidden similarities between successive distinct episodes allows you to link or bind these episodes to create a single super-ordinate category, e.g., several viewer-centred representations of a chair are linked to form a viewer-independent abstract representation of ‘chairness’. Consequently, the discovery of similarities and the linking of superficially dissimilar events would lead to a limbic activation — in order to ensure that the process is rewarding. It is this basic mechanism that one taps into, whether with puns, poetry, or visual art.

Partial support for this view comes from the observation that these mechanisms can go awry in certain neurological disorders. In Capgras syndrome, for instance, connections from the visual ‘face region’ in the inferotemporal cortex to the amygdala (a part of the limbic system where activation leads to emotions) are severed so that a familiar face no longer evokes a warm fuzzy emotional response (Hirstein and Ramachandran, 1997). Remarkably, some Capgras patients are no longer able to link successive views of a person’s face to create more general perceptual category of that particular face. We suggested that in the absence of limbic activation — the ‘glow’ of recognition — there is no incentive for the brain to link successive views of a face, so that the patient treats a single person as several people. When we showed our Capgras patient DS different photos of the same person, he claimed that the photos were of dif-

ferent people, who merely resembled each other! One might predict, therefore, that patients like DS would also experience difficulty in appreciating the metaphorical nuances of art, but such a prediction is not easy to test.

An Experimental Test

We conclude by taking up the final test of any theory: does it lead to counterintuitive predictions that can be tested experimentally? One approach — albeit a laborious one — would be to do ‘psychophysics’ on artistic experience: show people different types of pictures to see what they find pretty. The principles outlined above are difficult to test individually, but we believe that the very first one — the peak shift principle — can be tested directly. To do so one could measure the galvanic skin response (also known as skin conductance response, SCR) of naive experimental subjects to photos and drawings or caricatures. When you look at any evocative picture, the image is extracted by the ‘early’ visual areas and sent to the inferotemporal cortex — an area specialized for detecting faces and other objects. Once the object has been recognized, its emotional *significance* is gauged by the amygdala at the pole of the temporal lobe and if it is important the message is relayed to the autonomic nervous system (via the hypothalamus) so that you prepare to fight, flee, or mate. This in turn causes your skin to sweat, producing changes in its electrical resistance — a skin conductance response. So every time you look at your mother or even a famous face such as Einstein’s or Gandhi’s, you will get an SCR, but not if you look at an unfamiliar face, or a chair or a shoe (unless you happen to have a shoe fetish!).

So the size of the SCR is a direct measure of the amount of limbic (emotional) activation produced by an image. It is a better measure, as it turns out, than simply asking someone how much emotion he feels about what he is looking at because the verbal response is filtered, edited, and sometimes censored by the conscious mind — so that your answer is a ‘contaminated’ signal. Indeed there are patients with damage to the inferotemporal cortex who cannot consciously recognize their mother, yet will still register a larger SCR to her face than to unfamiliar people (Bauer, 1984; Tranel and Damasio, 1985; 1988). Conversely, we have shown that another type of patient has the opposite problem: he consciously recognizes her, but gets no emotional/limbic response to her and hence creates the delusion that she is some sort of impostor (Hirstein and Ramachandran, 1997). These examples suggest that measuring SCR somehow allows you to directly access those ‘unconscious’ mental processes. The responses we get to art objects may similarly be only partly available to conscious experience. You may deny you are attracted to a chap for all sorts of socio-cultural reasons but your hidden attraction to him may manifest itself as a large SCR to his photo (or sometimes, it may spill over when you dream during REM sleep)!

Our experiment, then, is quite simple. Compare a subject’s SCR to a *caricature* or even just an outline drawing of, say, Einstein or Nixon to his SCR to a *photo* of Einstein or Nixon. Intuitively, one would expect the photo to produce a large SCR because it is rich in cues and therefore excites more modules. One might find, paradoxically, that the drawing actually elicits a larger SCR, and if so, this would provide evidence for our ideas on the peak shift effect — the artist has unconsciously produced a super stimulus. As a control, one would show photos which have been morphed to look strange to ensure that it was not merely the strangeness of the carica-

ture which was producing the larger SCR. Similarly, one could also compare the magnitude of an SCR to caricatures of women (or indeed, to a Chola bronze nude or a Picasso nude) with the SCR to a photo of a nude woman. It is conceivable that the subject might claim to find the photo more attractive at a conscious level, while registering a large ‘unconscious aesthetic response’ — in the form of a larger SCR — to the artistic representation. That art taps into the ‘subconscious’ is not a new idea, but our SCR measurements may be the first attempt to test such a notion experimentally.

Another ‘experiment’ on art could take advantage of the fact that many cells in the inferotemporal cortex of monkeys respond selectively to monkey (and human!) faces — sometimes selectively just to a single face (Tovee *et al.*, 1996). Again, one could try confronting the cell with a drawing or caricature of the particular monkey (or human) face it was responding to. Would the cell respond even more vigorously to a ‘superstimulus’ of this kind?

Conclusion

In summary, we have identified a small subset of principles underlying all the diverse manifestations of human artistic experience. There are undoubtedly many others (cf. the principle of visual repetition or ‘rhythm’), but these eight principles are a good place to start. We shall call them ‘the eight laws of artistic experience,’ based on a loose analogy with the Buddha’s ‘eight-fold path’ to wisdom and enlightenment. One, the peak shift principle; not only along the form dimension, but also along more abstract dimensions, such as feminine/masculine posture, colour (e.g. skin tones) etc. Furthermore, just as the gull chick responds especially well to a super beak that doesn’t resemble a real beak, there may be classes of stimuli that optimally excite neurons that encode form primitives in the brain, even though it may not be immediately obvious to us what these primitives are. Two, isolating a single cue helps the organism allocate attention to the output of a single module thereby allowing it to more effectively ‘enjoy’ the peak shift along the dimensions represented in that module. Three, perceptual grouping to delineate figure and ground may be enjoyable in its own right, since it allows the organism to discover objects in noisy environments. Principles such as figure–ground delineation, closure and grouping by similarity may lead to a direct aesthetic response because the modules may send their output to the limbic system even before the relevant objects has been completely identified. Four, just as grouping or binding is directly reinforcing (even before the complete object is recognized), the extraction of *contrast* is also reinforcing, since regions of contrast are usually information-rich regions that deserve allocation of attention. Camouflage, in nature, relies partly on this principle. Five, perceptual ‘problem solving’ is also reinforcing. Hence a puzzle picture (or one in which meaning is implied rather than explicit) may paradoxically be more alluring than one in which the message is obvious. There appears to be an element of ‘peekaboo’ in some types of art — thereby ensuring that the visual system ‘struggles’ for a solution and does not give up too easily. For the same reason, a model whose hips and breasts are *about* to be revealed is more provocative than one who is completely naked. (E.g., in Plate 6 the necklace just barely covers the nipples and the dress is almost sliding off the hips.) Six, an abhorrence of unique vantage points. Seven, perhaps most enigmatic is the use of visual ‘puns’ or metaphors in art. Such visual metaphors are probably effective because dis-

covering hidden similarities between superficially dissimilar entities is an essential part of all visual pattern recognition and it would thus make sense that each time such a link is made, a signal is sent to the limbic system. Eight, symmetry — whose relevance to detecting prey, predator or healthy mates is obvious. (Indeed, evolutionary biologists have recently argued that detecting violations of symmetry may help animals detect unhealthy animals that have parasites.)

One potential objection might be that originality is the essence of art and our laws do not capture this. But the flaw in this objection becomes apparent when you consider the analogy with language. After all the ‘deep structure’ of language discovered by Chomsky has enormously enriched our understanding of language even if it doesn’t explain Shakespeare, Valmiki, Omar Khayyam or Henry James. Likewise, our eight laws may help provide a framework for understanding aspects of visual art, aesthetics and design, even if they don’t necessarily explain the evocativeness or originality of individual works of art.

In conclusion, we suggest that a great deal of what we call art is based on these eight principles. We recognize, of course, that much of art is idiosyncratic, ineffable and defies analysis but would argue that whatever component of art is lawful — however small — emerges either from exploiting these principles or from a playful and deliberate violation of them. We cannot resist concluding with a joke: A young man brings his fiancée home to introduce her to his father. His father is astonished to note that she has a clubfoot, a squint, a cleft palate and is hunchbacked, and can hardly conceal his dismay. Noticing his father’s reaction, his son calmly tells him, ‘Well Dad, what can I say? You either like a Picasso or you don’t.’

Acknowledgements

We thank Diane Rogers-Ramachandran, Francis Crick, Odile Crick, Julia Kindy, Mumtaz Jahan and Niki de Saint Phalle for stimulating discussions on numerous topics straddling the boundary between art and science. VSR also thanks All Souls College, Oxford, for a fellowship that allowed him to complete this project.

References

- Allman, J.M. and Kaas, J.H. (1971), ‘Representation of the visual field in striate and adjoining cortex of the owl monkey’, *Brain Research*, **35**, pp. 89–106.
- Arnheim, R. (1956), *Art and Visual Perception* (Berkeley, CA: University of California Press).
- Attneave, F. (1954), ‘Some informational aspects of visual perception’, *Psychological Review*, **61**, pp. 183–93.
- Barlow, H.B. (1986), ‘Why have multiple cortical areas?’, *Vision Research*, **26** (1), pp. 81–90.
- Bauer, R.M. (1984), ‘Autonomic recognition of names and faces in prosopagnosia: a neuropsychological application of the Guilty Knowledge Test’, *Neuropsychologia*, **22**, pp. 457–69.
- Churchland, P.S., Ramachandran, V.S. and Sejnowski, T.J. (1994), ‘A critique of pure vision’, in *Large-scale Neuronal Theories of the Brain*, ed. C. Koch and J.L. Davis (Cambridge, MA: The MIT Press).
- Crick, F. and Koch, C. (1998), ‘Consciousness and neuroscience’, *Cerebral Cortex*, **8** (2), pp. 97–107.
- di Pellegrino, G, Fadiga, L., Fogassi, L.; Gallese, V. and Rizzolatti, G. (1992), ‘Understanding motor events: a neurophysiological study’, *Experimental Brain Research*, **91** (1), pp. 176–80.
- Gombrich, E.H. (1973), ‘Illusion and art’, in *Illusion in Nature and Art*, ed. R.L. Gregory and E.H. Gombrich (New York: Charles Scribner’s Sons).

- Hirstein, W.S. and Ramachandran, V.S. (1997), 'Capgras Syndrome: A novel probe for understanding the neural representation of the identity and familiarity of persons', *Proceedings of the Royal Society of London*, **264**, pp. 437–44.
- Hubel, D.H. and Wiesel, T.N. (1979), 'Brain mechanisms of vision', *Scientific American*, **241**, pp. 150–62.
- Johansson, G. (1975), 'Visual motion perception', *Scientific American*, **232**, pp. 76–8.
- Julesz, B. (1971), *Foundations of Cyclopean Perception* (Chicago, IL: University of Chicago Press).
- Livingstone, M.S. and Hubel, D.H. (1987), 'Psychophysiological evidence for separate channels for the perception of form, color, movement and depth', *Journal of Neuroscience*, **7**, pp. 3416–68.
- Marr, D. (1981), *Vision* (San Francisco, CA: Freeman and Sons).
- Penrose, Roland. (1973), 'In praise of illusion', in *Illusion in Nature and Art*, ed. R.L. Gregory and E.H. Gombrich (New York: Charles Scribner's Sons).
- Pinker, S. (1998), *How the Mind Works* (New York: William Morrow).
- Ramachandran, V.S. (1990), 'Visual perception in people and machines', in *AI and the Eye*, ed. A. Blake and T. Troscianko (Chichester: Wiley).
- Ramachandran, V.S. and Hirstein, W. (1997), 'Three laws of qualia: Clues from neurology about the biological functions of consciousness and qualia', *Journal of Consciousness Studies*, **4** (5–6), pp. 429–57.
- Ramachandran, V.S. and Blakeslee, S. (1998), *Phantoms in the Brain* (New York: William Morrow and Co).
- Ramachandran, V.S., Armell, C., Foster, C. and Stoddard, R. (1998), 'Object recognition can drive apparent motion perception', *Nature*, **395**, pp. 852–3.
- Shepard, R. (1981), In *Perceptual Organization*, ed. M. Kubovy and T. Pomerantz (New Jersey: Lawrence Erlbaum).
- Singer, W. and Gray, C.M. (1995), 'Visual feature integration and the temporal correlation hypothesis', *Annual Review of Neuroscience*, **18**, pp. 555–86.
- Snyder, A. and Thomas, M. (1997), 'Autistic savants give clues to cognition', *Perception* **26**, pp. 93–6.
- Tinbergen, N. (1954), *Curious Naturalists* (New York: Basic Books).
- Tovee, M.J., Rolls, E. and Ramachandran V.S. (1996), 'Rapid visual learning in neurons in the primate visual cortex', *Neuroreport*, **7**, pp. 2757–60.
- Tranel, D. & Damasio, A.R. (1985), 'Knowledge without awareness: An autonomic index of facial recognition by prosopagnosics', *Science*, **228**, pp. 1453–4.
- Tranel, D. & Damasio, A.R. (1988), 'Non-conscious face recognition in patients with face agnosia', *Behavioral Brain Research*, **30**, pp. 235–49.
- Van Essen, D.C. and Maunsell, J.H. (1980), 'Two-dimensional maps of the cerebral cortex', *J. Comp. Neurol.*, **191**, pp. 255–81.
- Zeki, S. (1980), 'The representation of colours in the cerebral cortex', *Nature*, **284**, pp. 412–18.
- Zeki, S. (1998), 'Art and the brain', *Proceedings of the American Academy of Arts and Sciences*, **127** (2), pp. 71–104. Reprinted in *Journal of Consciousness Studies*, **6** (6–7), pp. 76–96.