Art and Neuroscience

s early as 1550, Giorgio Vasari wrote in his preface to Lives of the Greatest Painters, Sculptors and Architects that "even artists" have been able to see "how art, from its origins, reached the pinnacle of greatness and how from such heights, it fell into the depths of decline. Artists have thus understood its nature which, like the human body, goes through the cycle of birth, growth, old age and death" [1]. Indeed, art history started with a reference to the human body and the evolution it goes through. This was the beginning of the dialogue with the life sciences and it was to continue in the centuries that followed. In the wake of the encyclopedists, nineteenth-century authors gave up the all-too-easy metaphor of a growing organism and came to prefer the concept of an evolution of forms, reminiscent of the evolution of species based on principles inspired by the laws of anatomy formulated by Lamarck and Cuvier and by Darwin's theories [2]. The same time period saw the beginnings of experimental and quantitative analyses of the processes of perception [3]. "Physiological aesthetics" began to rank among scientific disciplines and has continued to develop since that time.

In the twentieth century, the emphasis shifted essentially to erudition, iconology, sociology and psychoanalysis, whereas the sciences dealing with the nervous system and its functions developed independently. This divergence was temporary, since the works of Focillon [4] and, above all, Gombrich [5] soon showed a definite return of interest for biological sciences in the field of art criticism. Gombrich, whose work is both rich and prolific, explored the relationship between visual perception, knowledge and pictorial images, and investigated the domain of artistic creation, which, for him, cannot possibly shun the laws of nature. "In art history, the word 'evolution' is a good deal more than a metaphor," Gombrich has written, adding that it could actually be accounted for "in Darwinian terms: form adapts to function through a process of mutation and selection, and then of survival of the fittest forms" [6].

The purpose of this paper is to encourage the world of research to pursue the work initiated by Gombrich. This can be achieved by investigating the possible neural origin of aesthetic pleasure and artistic creation, and jointly by reevaluating the evolution of a given painting, which presents formal analogies with the evolution of the species but clearly differs from it on several counts.

It is tempting to explore the neural element in art in the wake of my recent attempts at synthesizing knowledge concerning the central nervous system of both humans and animals [7], but the task may appear overambitious and some may think it violates the rules of conduct that the scientist assigns to him or herself. This is why I will repress the ambitious impulse to put forth my views as authentic scientific hypoth-

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eses, subject to refutation; my purpose will simply be to collect proposals coming from various disciplines that take the data of science into account and present them to you in argumentative fashion. In a word, I shall try to act as a philosopher [8] in the eighteenth-century sense of the word.

In order to facilitate my demonstration, I will make frequent reference to a painting, the *Lamentation on the Body of Christ*, attributed to Jacques de Bellange, which is to be found in the Hermitage Museum (Fig. 1).

ABSTRACT

I he author's intention is to foster further neuroscientific research in the field of art criticism, such as investigations of the possible neural origins of aesthetic pleasure and artistic creation. He conducts such an investigation through reference to a painting by Jacques de Bellange, discussing and analyzing topics such as mental evolution and the faculty of recognition as they relate to the perception and creation of art and the establishment of aesthetic conventions.

FROM SENSATION TO RECOGNITION

According to Spinoza, "Man's judgement is conditioned by the make-up of his brain" [9]. It is also with his brain that the human contemplates a painting. Physically speaking, a painting can be defined as a differentiated distribution of colors on a flat surface. When confronted directly with the Lamentation, the eye captures physical data on the colored surface and the light radiations it gives off, then converts them into electrical impulses that travel to the brain and its cortex. There, progressively, a mental object [10], an inner representation of the painting, will take shape. This construction begins, in fact, with a dissection. The form, color, location in space (which is here simulated by the painter by means of successive shadings of shadow and light) and movement (here, that of the eye of the viewer) pertaining to the various figures and objects in the painting will be analyzed separately. Distinct pathways and cortical areas of the visual system, both primary and secondary, located in the posterior (occipital) part of the brain, play a role in the way these features are processed [11].

This process of analysis is followed by a synthesis, the details of which have been the object of remarkable studies in the case of the perception of colors [12]. Indeed, whether one visits the exhibit at noon, when it is lit by natural light, or

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at night, when the painting is illumined by artificial light, the colors of the Lamentation appear almost the same, in spite of the fact that the spectral composition of the light reflected by the painting varies with the time of day. The fact that the perception of colors remains constant has preoccupied many physiologists since Helmholtz. It means that the brain extracts an invariant property of the colored surface from the energies of the light reflected by the painting. That property, as we know it today, is reflectance, the capacity of reflecting various wavelengths differentially. In other words, the brain reconstructs, from an external invariant, an internal invariant representing the color perceived. In accordance with these views, Zéki [13] has identified neurons in the cerebral cortex of a monkey (which perceives colors in much the same way as we do) that do not respond to the wavelengths actually received by the eye (which vary according to the time of day), but code for color as we perceive it.

In other words, the distribution of colored pigments laid on the canvas by the painter can be related to a measurable physical state of the brain that can be considered one of those "qualitative mental states," or *qualia*, that have constantly preoccupied philosophers [14].

The analysis/reconstruction of a painting involves multiple areas of the brain in addition to those that specialize in the perception of colors. The neurons in these areas are mobilized together with those of the neighboring cortex, which are engaged in the task of analyzing the aforementioned attributes of form, distribution in space and movement [15]. The analysis is completed by a synthesis. But whereas analysis may be a passive process, synthesis implies an "active" focalization of the viewer's attention. The painting as a mental object takes shape progressively.

The faculty of "recognition" is situated on a higher organizational level than that of perception. The problem is no longer to "represent" a face (or an object), but to identify it and spot it in a painting. What is it? Where is it? Cortical areas, which are distinct from visual areas, are located in front of visual areas in the temporal and parietal regions. These cortical areas participate in the work of recognition and spatial localization [16]. Neurologists have described a curious defect in certain patients, called prosopagnosia, or the incapacity to recognize and name faces [17]. These subjects present no apparent signs of intellectual deterioration nor of language disorder. They can easily identify ordinary objects or family pets, but they cannot manage to recognize and name a candidate for election whose photograph is reproduced on a poster, even if they have already seen him and know him by name. If a prosopagnosic had seen the Lamentation soon after it was painted, he or she would not have been able to identify the donor located in the right-hand part of the painting who, at the time, must have been a well-known church dignitary. Very precisely delimited lesions of the cerebral cortex result in prosopagnosia. Moreover, each of us has experienced the existence of several successive stages in recognizing faces, among which is the instance of being temporarily hampered by a fortuitous mental block: we know the face for a fact, but cannot remember whose it is at all, or we cannot recall the place we last saw the person or, more often than not, remember his or her name. Each of us also knows that several stages in this process can take place without our being aware of it or can even trigger an (unconscious) emotional response without our knowing it.

The "seed" of this recognition was found in a macaque [18]. Recordings were made in a precise area in its temporal cortex of individual neurons that responded to the view of a familiar face (the experimenter's) full front, but not in profile (or the opposite), to various facial expressions and to certain characteristics such as hair, eyes or the direction of the experimenter's gaze (which is more difficult to recognize). The functional specialization of each of the cells recorded is astonishing (Fig. 2). Even if such recordings have not been made in humans, everything leads us to believe that homologous neurons, sometimes called gnostic units, exist in the human brain and that their state of activity changes when our eyes move towards the faces of the figures or the objects that make up the composition of a painting.

For Mishkin et al. [19] these neurons, activated selectively by one face or object, are an integral part of a flow of information moving from neuron to neuron from the visual regions towards the temporal lobe, which makes it possible to answer the questions, "What is this figure?" or, "What is this object?" Another flow moves toward the parietal lobe to define the spatial relationship between these figures or objects and to specify what their relative movements are, if there are any [20]. The progressive mobilization of more and more specialized neurons, situated hierarchically above the visual areas, extends the internal representation of a painting to the larger domain of the cerebral cortex. In addition, a functional asymmetry develops between the two hemispheres of the human brain: the right hemisphere carries out spatial exploration, preferentially, but not exclusively, whereas the left hemisphere assembles complex images [21]. The gnostic cells gather to form assemblies or populations that participate in the recognition of more and more complex figures. At the same time, they extract more and more global characteristics from the figures in the painting. Little by little this leads to abstraction, or even to conceptualization of the colored shapes as figures and of the figures as a whole composition.

AESTHETIC PLEASURE

Bellange's work is a good deal more than a living painting of people bemoaning a death; it is not the mere imitation of nature, or mimesis. It is a rhythmical synthesis of forms and figures with what Gombrich calls a "chorus effect" [22] binding together the characters in the scene. "Catching a glimpse," in Diderot's words, of the relationships (apercevoir les rapports) [23] and capturing what binds the characters together is a dynamic act [24] that involves exploring the picture with the eye. Understanding the painting implies that one seizes the rhythm of forms and figures and identifies some sort of temporal organization. For that reason the process at work is akin to that of reasoning.

The scientific model, characterized by a restriction of the signified, aims at being the delineated representation of an object or a natural process; this representation has to be coherent, efficient and universal. It must be validated by experience but it may also be revised. The work of art differs from it because of its dual function [25]. Besides its role as an image, it has a symbolic function that becomes intelligible through a tacit underlying knowledge, which is but the expression of a particular culture at a particular moment in its history [26]. The reaction of a Tibetan monk to the Lamentation cannot possibly be the same as that of the donor for whom it was conceived. The former will understand, of course, the painful meditation upon death, but he will not understand the references to the Christian tradition as manifested in the crown of thorns or the



Fig. 1. The Lamentation upon the Dead Christ, oil painting ascribed to Jacques-Charles de Bellange, 1.16×1.73 m (Hermitage Museum, Saint Petersburg).

wounds of Christ, deliberately placed there as further sources of meaning, unless he has a profound and seasoned knowledge of Western culture. The painting is endowed with a plurality of meanings (polysemy), sometimes mutually exclusive, which become intelligible only if the viewer has been impregnated with Western culture and if, generally speaking, the viewer has accumulated information in his or her long-term memory.

If Watson and Crick had not discovered the double helix structure of deoxyribonucleic acid (DNA), or Einstein the theory of relativity, other scientists would have achieved the same results. Only their specific approaches to the problems would have been different. According to G.G. Granger, "The structures of science are posited as forms of denial of the individual case," even if "the latent structuration of scientific activity, as it is experienced by the scientist," bears the seal of his or her individuality [27]. The work of art, on the contrary, partakes of an "intersubjective" form of communication in which the individuality of the artist and that of the viewer both play a central role. Each work is characterized by a composition, an interplay of shapes and colors and "a superposition and a tangle of codes" that define the style of the painting [28] and are the signature of the painter's work.

A painting offers a plurality of meanings and is coded in many ways; for this reason, viewing it is in no way an act of passive submission. Quite the contrary: the various meanings it contains are not necessarily apprehended simultaneously by the viewer. They come to the viewer's mind one by one but they do not follow each other according to the precepts of universal logic, as is the case with scientific reasoning. The painting is endowed with a power of evocation that has to do with the meanings that correspond to what Granger calls the "strategic reasons" of the painter. It challenges the viewer who hypothesizes in order to rediscover those reasons and who, according to Gombrich, "duplicates in his mind the prowess of the imagination accomplished by the painter" [29]. Thus, viewing the painting becomes a re-creation, in the process of which the hypotheses brought forth by the painting are put to the test. They echo each other and are preserved, or, if they are not, they are either corrected or discarded. Shapes, images and clues suggest meanings that, in some cases, may not have been part of the artist's intentions and simply originate in the viewer's longterm memory, resulting from personal experiences. The painting affects this stock of unconscious memories and brings them to the surface by focusing the viewer's attention on the compartment of conscious short-term memory. An imaginary dialogue starts with the painting. It becomes a "shared dream"; its power over the imagination becomes particularly strong when the image is not mere mimesis and the viewer can distance him or herself from the painting. Whereas the scientific concept is possessed of a precise meaning and aims from the start at universality, the work of art, because of its power of evocation, opens out on a plurality of intellectual speculations in which subjectivity and individual experience play a major role.

Viewing a painting involves the highest of functions in the hierarchy of the brain, that of reason, because it necessitates a perception of the global rhythm of shapes and forms and an assessment of the stylistic code-as well as of the numerous levels of symbolic interpretation-and also because it is endowed with the faculty of simulation [30]. Marcuse, paraphrasing Hegel, wrote, "Behind the aesthetic form, one finds the harmony of sensuality and reason" [31]: Schiller stated that the work of art "reconciles the laws of reason with the interests of the senses" [32]. Of course, pleasure cannot be defined in terms of formal concepts. But the fact that artistic representation involves reason has a major impact on the notion of pleasure. According to Plotinus, it is intelligible music that creates sensitive music. The daily experience of scientists, even those working on the most abstract ideas [33], illustrates the impact of the discovery of a new concept on their emotional makeup. Many claim that they constantly resort to aesthetics in their research activities. A painting is likely to affect us because it echoes hypotheses that have to do with its meaning, but above all because it echoes the hypotheses concerning pleasure that anyone can formulate inwardly, consciously or not, and that can be called desires.

In that respect, the emotional impact of the Lamentation is particularly strong since it has to do with death. But death appears here in a form that contradicts its real nature. The body of Christ presents none of the rigidity of a corpse. The painter changes it into a supple, harmonious living body, whose every muscle vibrates under the skin by candlelight. To take up Kenneth Clark's words about Michelangelo's Pietà, the artist "gave Christ such refined physical beauty that we hold our breath as if we wanted to arrest the passage of time" [34], to stop the irreversible decay of the body and preserve in ourselves the joy and comfort of the mother's breast towards which Christ tenderly leans his head. However tragic the scene may be, the Lamentation affects us because of the distance the artist has created between our knowledge of death and the joy we derive from the creation that lives in our minds.

THE VARIOUS ARCHITECTURES OF AESTHETIC PLEASURE

The deciphering of the neural organizations of reason is just beginning [35]. However, several converging studies emphasize the importance of a number of complex and heterogeneous areas in the brain cortex located in the frontmost part of the brain, or the frontal lobe [36]. Its area increases in size in spectacular fashion from primitive monkeys to man, and for that reason, it has been called the organ of civilization. In order to describe the impact of lesions of the frontal lobe, the neurologist Alexandre Luria decided to use a painting as a test [37]. To patients suffering from dysfunction of the frontal lobe, Luria showed a reproduction of a painting by Baron Klodt, The Last Spring, the original of which is at the Tretiakov Gallery in Moscow. "It represents a dying girl sitting in an armchair while her elderly parents watch her sadly and her sister stands by the window in an attitude of profound sorrow" [38]. Luria underlines a patient's difficulties in understanding the painting. He describes how the patient suddenly stares at the girl's gown and interprets the subject of the painting as a wedding scene. The patient's global evaluation of the emotional elements of the painting is erroneous. He stares at certain details with "steady and arbitrary" concentration, which results in impulsive and fragmentary judgments that are in no way inhibited or criticized. The element-by-element analysis does not open out on a synthesis, particularly when the images are presented to the patient successively in time. This observation, together with many others, suggests that the frontal cortex plays a role in the perception of the overall organization of the figures in the painting, as well as in the comprehension of its various levels of meaning. It seems in particular to play an essential role in the attribution of mental states, affects, beliefs, desires and intentions by the patient both to his or her fellow patients and to abstract representations of them. According to Goldman-Rakic, the prefrontal cortex "keeps in line" the pertinent mental representations (stocked in the temporal and parietal areas) that are needed for a suitable synthesis; it also eliminates non-pertinent responses [39].

The same frontal lobe patient, submitted to a test with playing cards called the Wisconsin Card-Sorting Test [40], does not become aware of the tacit changes

in his partner-examiner's strategy. It takes him much more time to understand them than it takes the normal subject to understand, and he perseveres in his mistakes. He performs "routine" tasks normally but he no longer has a "supervisory attentive" system [41], which enables the normal subject to think up new cognitive strategies when confronted with unexpected situations, to select appropriate response patterns and also to detect possible errors that may thwart the accomplishment of a project. It would appear then that the frontal cortex intervenes both in the genesis of hypotheses and in the elaboration of critical judgment, both faculties being essential for viewing a painting, as we have seen.

These interpretations have a strong neural basis. It is true that the monkey's frontal cortex is less developed than the human's; nonetheless, cells capable of anticipating a motor act have been found in that area [42]. Their activity precedes the task to be carried out, sometimes by a few seconds. In certain experimental situations, the activity of a given neuron does not depend on the precise nature of the task itself but on the temporal context in which it is performed. These cells distinguish between what has been done and what remains to be done [43].

The elucidation (still in the process of study) concerning the connectivity of the frontal cortex reinforces these conclusions [44]. The superior capacity of integration of the frontal lobe is due to the fact that it sets up reciprocal connections with the temporal and parietal regions that, in turn, receive signals from the visual areas. The frontal lobe ranks at the top of the hierarchy insofar as the connections of the whole of the cerebral cortex are concerned. Because of this, the frontal cortex carries out "second degree" operations, to use Piaget's term, or, if one goes along with Kant, it achieves the synthesis of the concepts produced by understanding.

As early as 1868, in the first description he made of the frontal syndrome, Harlow pointed out the existence of serious emotional disorders whose modalities differed from one hemisphere to the other [45]. Once again, these disorders can be explained objectively if the connectivity of the prefrontal cortex is examined. Indeed, the prefrontal cortex sets up fruitful connections with an underlying group of structures and nervous circuits referred to as the limbic system [46]. This "brain of the emotions" is involved in controlling the subject's moods [47]. Stimulating certain zones of the limbic system with electricity can arouse pleasant sensations that, in animals, lead to frantic self-stimulation. Stimulating other areas of the limbic system will produce the effect of a punishment. These precisely delimited areas, involved in pleasure or in its opposite, repulsion, can be clearly distinguished from the nervous structures that intervene in the satisfaction of the much more primary drives of hunger, thirst or sex, which are to be found in the hypothalamus.

Going into daring speculations is out of the question. Nevertheless, it seems legitimate to suggest that aesthetic pleasure calls into play, in a concerted manner, ensembles of neurons that unite the most synthetic mental representations, elaborated by the frontal cortex, with precise activity of the limbic system. To this effect, Nauta has suggested that the frontal cortex, in addition to its function as generator of hypotheses and future conduct, also anticipates emotional or affective states that are likely to accompany the realization of those projects [48]. The frontal cortex marks out the organization of a sequence of representations (a process of reasoning) and of emotional points of reference, and accordingly, it contributes to the faculty of being stimulated, symbolically as well as emotionally, by a painting. It enables the viewer to "put himself in the place" of the figures in the painting and to express "empathy" [49]. In these conditions, aesthetic pleasure apparently results from the initiation of a resonance as well as from the concerted mobilization of groups of neurons located on several levels of cerebral organization of the brain, from the limbic system to the frontal cortex: a broadened mental object can achieve the "harmony of emotions and reason."

MEMORY AND MENTAL DARWINISM

The passage in time of a period of "exploration" of a painting, with its evocations of various levels of meaning and emotional states, can be labelled evolution—and even Darwinian evolution from several points of view, especially regarding the storage in memory of the meaningful elements of the painting [50]. We are dealing here with the evolution of physical states of the brain that have only indirect bearing on the genetic material of the body, at variance with the evolution of the species to which Darwin's name is attached. In the case at hand, evolutions take place, instead, in the viewer's brain on time scales (greatly differing from the scale of geological time) that can last from a tenth of a second to several years. These evolutions nevertheless do involve processes of multiplication or amplification, in particular when they have to do with the stability of the mental representations and their storage in the long-term memory compartment. These representations indeed can emerge from this compartment in order to help create new mental objects or to play a role in the creation of an intentional context, which will govern the concatenation of other representations. In other words, re-utilizing selectively stabilized representations is a form of multiplication.

Towards the end of the nineteenth century, Taine wrote:

In the struggle for life that constantly goes on among all the images we possess, the image that was originally endowed with the greatest energy maintains the capacity to overcome its rivals each time there is a conflict, according to the law of repetition that is the basis of that struggle [51].

And for American philosopher William James, "to think is to make selections" [52].

In its most general form, the Darwinian model is based on an internal generator of diversity that, in the case of mental processes, gives transitory and spontaneous birth to different combinations of active neurons (or pre-representations). The distribution of these neurons varies, with a random component, [53] from one instant to another. The generator also contains a selective mechanism that retains certain combinations while eliminating others. According to the proposed model, a prerepresentation will be stabilized if it echoes a perceptual representation brought about directly by interaction with the outside world. In the proposed model [54] the latent trace left in the brain by this echo brings about a change in the efficiency of the contacts between nerve cells, or even in the number of those contacts [55]. It is a matter of direct concern for us that this formal network of neurons also stores temporal sequences, or concatenations of representations in the memory. According to this model, which is still quite rudimentary, a painting, or rather the significant relationships present in it, is not stored in the memory in a passive manner, like the print left by a stamp on a piece of

wax. If storage is to take place, it requires active participation on the part of the viewer—alert anticipation, which is always situated in a definite context in time and space.

Experimental psychology has taught us, however, that the memorized configuration is integrated into a highly organized, hierarchical ensemble, a "taxonomic chart," a system of classification already in existence [56]. The processes of inserting data into this semantic space and extracting it later (faculties that are both exploited by mnemotechnical processes) are facilitated by the imagistic form of the configuration, but also because of its novelty. This last characteristic is of most particular importance in the viewer's interaction with the work of art. There is very little discrimination involved in the transitory passage of the representations perceived by the sensory organs through the shortterm memory. What is more, the capacity of this memory is small and it functions as a palimpsest [57]. The selection for long-term storage-the conversion of the active, transitory mental act into a latent, stable trace-at once excludes what is already extant. If a work of art were the identical representation of a natural object, its chances of leaving a trace in the long-term memory would be slim-perhaps non-existent. The figures it represents are natural enough to provide indications of meaning or hints necessary for semantic classification. But the peculiar artificial character of a work of art, underlined by the painter's style, provides the novelty and the distance necessary for it to be efficiently imprinted in the long-term memory.

Our recollection of a picture is always fragmentary. The fragments that come to the surface when the memorized trace is reactivated vary considerably from one experience to another over the space of several years or even several days. The variability of the result is a sign of the intrusion of a random component, both in the storage process and in the process of recollection. This variability can be explained, within the confines of the Darwinian model of neural storage, by the variability of the viewer's inner state and by the intrusion in the time sequence of the random element of sensory anticipation, which is likely to echo the particular characteristics of the painting. Access to the long-term memory compartment cannot be gained without definite constraints. It seems plausible that, among other cultural representations, a work of art distinguishes itself by the skillful exploitation of these constraints.

CREATION

The creation of a painting is not a mere symmetrical process of active contemplation. The creator no doubt possesses the ability to stimulate the public and help it store data in its selective memory, but artists also possess the rarer ability to produce public representation, "images and scenes in flat paintings" [58]. By means of movements of the hand, artists project images of their own inner worlds onto the two dimensions of a canvas. The passage from the image to the act is by no means instantaneous. For Gombrich, paraphrasing Constable, creating a painting is a kind of "scientific experiment" [59], it is the result of a complex development in time, an evolution-or, rather, a cascade of nested evolutions-that the painter undergoes in his or her dialogue with the canvas. To put it briefly, at least three forms of evolution can be distinguished; each can be interpreted within the framework of a Darwinian pattern, but also has its own modalities. They have to do with the elaboration of a pictorial intention (or, for Gombrich, a mental schema, with its progressive actualization through the mastering of one's gestures) and with the final accomplishment of an organized, coherent painting capable of withstanding the test of logic.

THE FUNDAMENTAL THOUGHT

Edgar Allen Poe described "the elaborate and vacillating crudities of thought ... the true purposes seized only at the last moment . . . the innumerable glimpses of idea that arrived not at the maturity of full view . . . the fully matured fancies discarded in despair as unmanageable . . . the painful erasures and interpolations" that make the first steps of the creative process a "mental experiment" of unmistakable Darwinian mould [60]. In a state of particularly keen expectation, the artist calls to mind images and representations, dissociating them only to combine them anew, sometimes almost without being aware of it, until the "ideal pattern," "the fundamental idea," as Delacroix described it [61] becomes set in his or her brain.

Time and again painters have recalled the intervention of chance, of accidental forms in the birth of this pictorial pattern. Thus Leonardo da Vinci spoke of the power of "vague shapes," like clouds or muddy water, to rouse the inventiveness of his mind [62]. But the idea of a painting does not loom out of the fog. The combinatorial creative mind works on pre-structured elements. The artist appeals to "mnemonic" images and representations, to a vocabulary of forms and figures that are stabilized in the connective organization of the brain (as is one's native language) during a long process of epigenesis, through a selection of synapses that imprint a particular mark on each individual [63]. In the sixteenth and seventeenth centuries the representation of man, often observed in real life, was the center of attraction. In addition, the painter borrowed from other paintings, including his or her own, that helped the painter, as Gombrich put it, to discover schematic elements that might be adapted to his subject [64] and to integrate the individual painting into a higher evolutionary order, about which more will be said later. The creative activity of the artist is reminiscent of the tinkering [65] that characterizes the early stages of mythical thought.

In the precise case of the *Lamentation* by Bellange, there are in actual fact striking analogies between his drawing of the body of Christ and an etching by Parmigianino on the same subject [66]. The similarities suggest that Bellange knew the work, and had in mind the schematic elements that he undoubtedly retained for his intended picture from the beginning. The two main figures seem to have been combined—the figure standing on the left has been eliminated and the candlebearer has been added—but the rhythmical link between the faces has been preserved.

One of the positive aspects of applying the Darwinian model to the creation of the pictorial schema is to compel us to define the criteria responsible for the painter's final choice. Reason here partakes of Granger's "strategic" reason, which bears on the plausibility of goals and ends [67]. The appropriateness of the theme to the dictates of the ecclesiastical dignitary and the awakening of the sentiments that it is likely to effect first in the painter, then in the viewerare contributing factors. Finally, the logical coherence between the elements of the painting surges as a whole in the painter's mind, like a revelation, just as the discovery of the solution to a problem "illuminates" [68] a mathematician's thinking.

Thus the variation and selection of intentions intervene at the highest level of the organization of the brain: that of reason. It therefore seems legitimate to suppose that the frontal lobe plays a major part in the creative process. It is common knowledge that the brain is the seat of considerable spontaneous activity, the form of which can be regulated selectively by an "internal" focalizing of the attention [69]. It is understandable, then, that in the region of the frontal lobe, transitory assemblies of active neurons, or pre-representations, are formed and remain in the conscious short-term compartment, or working memory (undoubtedly with the participation of selfsupported closed circuits) in order to compose a "fundamental thought," a mental simulation of the picture.

MASTERING THE GESTURE

For Vasari, "drawing is the sensitive expression, the explicit formulation of a notion within the mind or imagined in the minds of others and developed into an idea"; it is the projection of the painter's "fundamental thought" [70]. Drawings (even those of the greatest artists), with their gropings, corrections, pentimenti, trials and errors, show that a new Darwinian evolution is henceforth taking place between the sheet of paper and the painter's brain. The image drawn by the painter's trained hand becomes a visible image that is confronted with the pictorial intention. From this "trial," painters command a new gesture whose graphic manifestation is incorporated in the sketch, completing and enriching it. At that point they try new experiments, which lead them to discover new techniques, invent efficient formulas, define mathematical rules or simply put the methods they have learned from their masters into practice. The dialogue goes on from the first sketches to the drawing through "schemata and corrections" [71]. The only known drawing of the Lamentation (in the Musée des Beaux-Arts in Dijon), done with ink and wash, shows this, for it can be taken, in spite of its small size, as a rather precise modello of the final painting. The main protagonists, their expressions and their arrangement in space are already present, as are the subtle variegations of light and shadow that give the work its nocturnal quality.

At last the painter lays the definitive colors on the canvas. As Baudelaire wrote, "a harmonically composed painting consists of a series of superimposed paintings, each new layer giving the dream more reality" [72]. Discreet but meaningful variations illustrate the experiments that the painter has carried out in order to pursue the evolution up to the finished work: the body of Christ is redrawn to occupy a larger space in the final version; faces are added or even duplicated, full front or in profile, so that the final composition is a melody of faces around the mother grieving over the body of her son. The lighting on the faces has become violent and slanted so that they appear as negatives, and the background has become darker. A restructuration has taken place, achieved by concentration, emphasis on the fundamental elements and a rearrangement of facts. At each step, the artist becomes a demanding viewer who is concerned with the resonance of each dab of paint. The sketch is discreetly modified by the search for form, color and what Gombrich refers to as "graphic and pictorial illusions" [73] that tally with the artist's initial intention; in the process, logical coherence, rational integration and the "adjustment of the eye with reason" (in Chambray's words [74]) are tested repeatedly. The marks of this unique evolutionary process-the reworking, pentimento and superposition (which also distinguish the original from a copy)—are a record of the painter's specific techniques as well as the gestures the painter habitually uses to delineate his or her figures, to apply colors and to give the illusion of volumes. These marks are so many personal characteristics of the system of shapes and figures that express subjectivity and define his or her style.

NEURAL COMMAND OF THE PAINTER'S GESTURE

If the neural bases of the genesis of a pictorial pattern are still very enigmatic, those that control hand movements are better known [75]. The delicately coordinated movements of the fingers that control pencil marks or brush strokes are all commanded by cells found in specialized regions of the cerebral cortex called sensory motor areas, which send their orders (after they are relayed by the spinal cord) to the muscles that carry them out. The same areas in the brain also control the movements and orientation of the hand.

When the painter stands back from the painting he or she is working on, the painter's head and eyes change positions, while the painting, like the rest of the world around it, remains stable from



Fig. 2. Responses of single neurons from the temporal cortex of a monkey to face stimuli. Each of the nine pictures shows a stimulus; the corresponding response is shown below it. Each vertical bar represents a nerve impulse. The selectivity of the neuron to a complete face with two eyes is remarkable [125].

the painter's point of view. Other areas of the cortex previously mentioned, the parietal regions, contribute to the invariant reconstruction of the outer world by regulating visual attention. In a case of cerebral lesion the patient becomes visually disoriented to such an extent that he or she can no longer hit a given target precisely; the patient's graphic gestures become uncontrollable. He or she can no longer coordinate bodily space and visual space [76].

Still other areas in the central nervous system participate in guiding visual movement, particularly the cerebellum, which governs its progression like an internal clock. But the initial programming of motor movement is carried out before the motor cortex intervenes, in the frontal regions of the cortex where, supposedly, the initial thought of the creator is born and developed. In the monkey, certain neurons of this "premotor" cortex are released when the animal grabs food and carries it to its mouth. As Rizzolatti and his collaborators [77] have shown, these particular neurons are activated when an experimenter makes the same gesture in front of a motionless monkey: the same neurons intervene both in the "understanding" and execution of a gesture.

THE EVOLUTION OF CULTURAL MEMES

Unlike the evolution of species, the evolutionary dynamics of cultural objects have no direct effect on genetic inheritance [78]. They nonetheless present major formal analogies with the former, although these dynamics are located in the realm of interaction between individuals of a social group [79]. Cultural entities capable of being transmitted and propagated epigenetically from brain to brain in human populations, called "memes" by Dawkins [80] (from the word mimesis) have even been compared to viruses. (These entities have been called "culturgenes" by Lumsden and Wilson, "public representations" by Sperber and "cultural objects" by Cavalli-Sforza [81].) "If a fertile 'meme' is implanted in my brain," writes Dawkins, "it will literally become a parasite there, and transform the brain into a vehicle to propagate the 'meme' in the same way in which a virus lives as a parasite on the genetic mechanism of the host cell" [82].

This epidemiology of mental representations [83] is based on the stability of the memes. Their longevity can be explained by the fact that they are stored in the long-term memory and above all, in the case of a painting, by the fact that the representation stores cultural data in its materials, the latter being more stable and diverse than those of the human brain. Their stability is also based on the reliability of the meme's transmitting mechanism in the process of inter-cerebral communication. Similar to a gene, but on a very different organizational level, the meme becomes a replication unit that is transmitted from one generation to the next (such as a religious belief) or propagated from one individual to another within the same generation, as are technological innovations or scientific ideas [84]. Similar to a gene, it can evolve because of errors in duplication and "random" recombination. When the creative mechanisms of the memes, which are private mental objects, become public representations [85] they are compounded by new selective mechanisms.

For Cavalli-Sforza and Feldman [86] there are two steps in the selection of cultural objects: The first one is permissive and deals with information. It allows access to the compartment of the shortterm "working" memory of the receiver. The other one is active and deals with adoption or long-range incorporation into the brain of every individual in a social group and in the extra-cerebral cultural inheritance of a given community. The probability of acceptation [87] or of "cultural survival for survival's sake" [88] can then be defined quantitatively on the basis of criteria whose identification becomes the touchstone of the Darwinian model. Communication between members of the same social group is a supplementary constraint added to those that have already been mentioned, like expectation and the fact that storage in the long-range memory is relatively recent.

Shannon and Weaver's theory of information [89] postulates that communication consists of message transmission, which includes three steps: encoding, the propagation of signals and decoding. In these conditions, the elements transmitted are a very remote approximation of the thoughts of a given speaker. This process does not easily accommodate the case of myths or of works of art that communicate far more than their surface meaning because they are highly coded. Whence the necessity of appealing to a referential model that is located, insofar as its organization is concerned, on the level of reason, in which context plays a fundamental role. Context furnishes a body of hypotheses about the world that have a bearing on the interpretation of the models transmitted, and thus it defines, as it were, the "competence" of the receiver.

For Grice [90], communication between human beings brings the recognition of intentions into play but it also arouses new hypotheses in the interlocutor's mind. Sperber and Wilson developed this point by introducing the notion of the relevance of a message as an indicator of a multiplicative effect resulting from its combining with a former message [91]. In other words, the greater the power of a message to generate hypotheses, the more relevance it has. Like other anthropologists [92], Sperber is reluctant to use the Darwinian pattern in his "epidemiology of mental representations" [93]. In my opinion, however, it is legitimate to consider his notion of relevance as a criterion in the potential selection of a cultural representation. Selection would thus to a certain extent be based on the potential for cognitive "enrichment" contained in the message.

We are still a long way from being able to propose a neural model of selection

through relevance, but such an enterprise seems plausible in the wake of the studies done on intention [94]. We can understand that a mental object entering the short-term compartment of the memory will be all the more relevant if it has more possibilities of combining with other pre-representations or intentions already present in the compartment, to become part of a latent semantic ensemble by activating new combinations of neurons and arousing expectation.

A painting is a particular type of public representation that can be distinguished from factual representations bearing on everyday life [95] as well as from beliefs and scientific hypotheses. Its evolution differs from that of scientific memes in several ways. Throughout history, the concepts produced by science have become more and more effective in solving problems [96]; in other words, they have led to cumulative progress in the field of knowledge. This production is to be distinguished from that of the evolution of living creatures, which, throughout geological time, has resulted in a growing complexity of organization that is especially spectacular in the case of the brain. The evolution of art (like that of beliefs) has not been characterized by progress, even if throughout history it has incorporated scientific data or referred to it. As we look back over the centuries from our vantage point, Vasari's metaphor seems more and more unacceptable. Is it possible to speak of progress from Raphael to Caravaggio or from Nicolo dell'Abate to Nicolas Poussin? Paintings evolve by adaptive renewal of their forms, figures and themes; in my opinion, no real progress can be distinguished.

THE PAINTING AS A "Synthesis of Memes"

A painting is a meme of rare complexity or, rather, a complex synthesis of memes that are transmitted and propagated by the painter's brain from one painting to another in the work of a given painter and from the work of one painter to another. The work of a historian often consists of classifying the paintings in the work of a painter chronologically and defining schools and the relation between schools. This can be done, if there are no documents available, by looking for variable elements in a huge mass of invariants that characterize a painter's style or the style of a group of artists he or she belongs to. Historians try to retrace an evolution that, in the last analysis, is possible only because the painter borrows patterns, figures and forms, not only from him- or herself, but above all from others. These elements become so many units of replication, memes that are perpetuated throughout the ages.

The Lamentation is one of the most particularly striking illustrations of this (Fig. 3). According to Kenneth Clark [97] the origin of the Christian iconography of the entombment of Christ must be sought in Greco-Roman art, in the representations of the death of a hero: in particular, in a group sculpture to be found in the Capitol Museum in Rome, in which the dead hero is being carried off the battlefield by his comrades. During the Renaissance, Donatello, in the marble relief entitled The Dead Christ Supported by Angels (located in London at the Victoria and Albert Museum), introduced new intensity by straightening up Christ's torso and exalting his beauty, thus incorporating Greco-Roman mythology into Christian mythology with the greatest of ease. Independent of this movement, in the gothic art of Northern Europe, there exists a type of Pietà in which the dead body of Christ lies across the lap of his grieving mother, surrounded by John and Mary Magdalene; Clark has pointed out that the most accomplished example of this type is the Pietà in Villeneuve-les-Avignon.

In Parmigianino's etching, which probably was Bellange's main source of inspiration, the ancient and Christian components merge or, to borrow a term from genetics, recombine. The nightlike atmosphere and the lighting provided by a candle bearer are reminiscent of the Pietà by Rosso (in the Museum of Fine Arts, Boston) or of certain drawings by Primaticcio (such as The Mascarade of *Persepolis* in the Louvre). But the mood has changed and is closer to that of certain paintings by Hans von Aachen or by Spranger (see in particular his Risen Christ Triumphant over Death—an epitaph in honor of Nikolaus Müller-in the Narodni Gallery in Prague). In these works the background becomes darker and the body is lit in a violent manner. Two drawings by Hans von Aachen [98] on the theme of the dead Christ illustrate the relationships between the Lamentation and the School of Prague: there is the same attempt to use slanting light to delineate the contours of Christ's body [99] and there are analogies in the arrangement of lights and shadows in the composition as a whole [100].

However, in Bellange's work, the focus is on the body of Christ and the faces of

the Virgin and the donor, who are here shown in half length. In addition, the artist introduces a fantastic, even disquieting note by using beams of light di sotto in su on the faces and hands of the figures that loom out of a shadowless night. This composition and its chiaroscuro seem to have found fertile ground in Lorraine, since some 10 to 20 years later Georges de la Tour painted Irene Ministering to Saint Sebastian (also called the lantern portrait) [101], directly inspired by the Lamentation, with the main figures taking on the same poses and the same use of directive lighting. However, the arrow in Sebastian's left thigh and a tender expression on Irene's face are indicative of a change in the protagonists' identity. The conceptual universe of the painting has evolved in depth, moreover: several superfluous figures have disappeared, including the donor (whose presence in Bellange's scene from the past was most unlikely), and Irene's face now wears a truly pathetic expression. But the mysteriousness inherited from Bellange still pervades the picture, and contrasts with the provocative naturalism of Caravaggio's paintings, which de la Tour, the painter from Lunéville, probably never saw, and whose influence, if there ever was any, was undoubtedly less important than that of the Prague School.

This is but one example among many that serve to illustrate both the remarkable stability of "pregnant" [102] memes of form, with their strong emotional power, and their evolution, which results from two forms of combination: among themselves and with memes of meaning, which are subject to similar evolution. It is possible to see how the memes of form and meaning of the ancient world have successively adapted to the cultural contexts of the Renaissance and the Counter-Reformation. A painting is therefore subject to a longitudinal evolution of memes of form and a vertical crisscrossing (intersecting) of numerous memes of meaning, which the artist unites with the know-how that is the mark of his or her genius.

The oral transmission of memes of form from master to pupil or from colleague to colleague tends to standardize local art production and thus differentiate it from that of other geographical areas. The "open" dynamics of the propagation or diffusion of memes, which internationalize formulas, patterns and manners on smaller and smaller scales, are superimposed on the dynamics of division into schools, which are connected with geographical isolation. The movements of greater scope that characterize an era, like mannerism or classicism, emerge gradually and transcend the style of a given master or school.

THE SELECTION OF PERTINENT MEMES

Defining the criteria by which memes are accepted or adopted constitutes, as has been said, one of the positive contributions of the Darwinian model. A painting perpetuates an aesthetic message, but it is also a piece of merchandise for the general public and its sale provides the artist with a means of livelihood. Through the choices they make, buyers, patrons and benefactors of the arts become mediators of the cultural environment, of the tangled network of minute relations that any artistic product implies [103]. It is through them that, in the words of Taine, the "pressure of the surrounding public mind and manners" is exerted [104] as well as the interests of certain classes. This "pressure" does not necessarily preclude the pressure that the environment brings to bear on artists when they undertake a painting that may spontaneously incorporate memes similar in nature to those that determined the choices of a patron. Leroi-Gourhan has noted that

the double nature of art, which is both collective and individual, means that it is impossible to make a complete distinction between marketplace art and disinterested art, between art for some purpose and art for art's sake [105].

The church dignitary who ordered the *Lamentation* from Bellange would finally take the painting only if it fulfilled its function in the religious edifice that he had intended it for, only if it possessed the "convenance" that was so important for the painters of that period [106].

In the thirteenth century, John of Genoa wrote in his *Catholicon*,

Let it be known that there were three predominant reasons for the institution of images in churches. First of all, to instruct uneducated people for whom images serve as books. Secondly, so that the mystery of the Incarnation and the example of the Saints, by being exposed daily to our view, may act more powerfully on our memories. Thirdly, in order to encourage a feeling of devotion which is more efficiently aroused by means of things seen, rather than things heard.

The Catholic church, in particular after the Council of Trent, was to use images for historic and commemorative instruction, for edification and propa-

















ganda in its struggle against Protestantism. Thus, for the *Lamentation* and religious paintings in general, conformity with the Holy Scriptures and their illustrative and edifying nature were necessary but not sufficient criteria for acceptance.

Art, and particularly painting, as the selected example shows, has frequently been used to convey moral values. Ethics contribute to regulate the interactions between members of a social group. They are founded on theoretical representations of humanity in society and of models of social life that may or may not be propagated among human populations as so many "moral memes." Facilitating communication within a cultural group and, generally speaking, reinforcing social links (the Latin word religere, meaning "to link together," is the root for the word "religion") can thus influence the acceptance of the pictorial memes and moral memes with which they are associated.

Anthropologists and ethnologists have pointed out the frequent use of pictorial representations for the purposes of magic. For prehistoric man, the use of images probably testifies to, in Leroi-Gourhan's words, a "reflected vision of shapes" in which "the viewer is confronted with an organized image of his universe, an image of a relationship to objects that come into his field of perception" [107]. According to Lévi-Strauss, the use of images bears witness to a process of "systematization of sen-

Fig. 3. (left) Hypothetical evolutionary history of The Lamentation upon the Dead Christ, ascribed to Jacques-Charles de Bellange. According to Kenneth Clark [126] such representations of the entombment of Christ (or of the Pietà) derive from a Greco-Roman motif of the "death of the hero," exemplified here by a funerary stone from the Capitole Museum in Rome, often referred to as the Military Pietà (top). The composition of the Lamentation may be viewed as a "recombinant" between an Italian type such as The Dead Christ and the Angels by Donatello (Victoria and Albert Museum, London), which was reutilized by Giovanni Bellini and others (second row, right) and a gothic type such as the Pietà from Villeneuve-les-Avignon (Louvre, Paris) where the body of Christ lies upon the knees of his mother (second row, left). An etching by Parmigiano (third row, left) and two drawings by Hans von Aachen (third row: center, right) may have inspired the Lamentation (fourth row), from which the Saint Sebastian by Georges de la Tour (copy at the Rouen Museum) seems to derive directly (bottom).

sory data" with the objective of acting on the world of nature and protecting man from it. In the first stages of the development of thought, a true physical causality of natural events had not yet been discovered. The "immaterial and mysterious" power attributed to images acted as "a means of imaginary intervention" against the hostility of nature, in particular, in cases of illness [108]. It may well be that the Lamentation had a magic power over death in the eyes of the viewers of that period, as perhaps it has even for certain viewers in our time. The belief in the magic power of images probably functioned as a factor in the selection of pictorial memes, but it was also a motivation for numerous iconoclasms to destroy them systematically.

The combination of memes of form with memes of meaning—with hypotheses about the world, beliefs and ideologies as well as with scientific knowledge contributes to the constant updating of works of art and to their ceaseless renewal. But the final choice of a painting by a patron, a benefactor or an art lover depends, in the last analysis, on its emotional relevance to the individual and to the community. Consciously or unconsciously, the painter uses forms, rhythms and technical processes that exercise a strong emotional power over the painter as well as the viewer.

HOMO SAPIENS' PREDISPOSITIONS FOR ART

The predispositions of the human brain not only allow for the evolution of painting through the renewal of pictorial memes, but also limit it. There are numerous examples in the animal world of an emotional state or behavior triggered by a certain shape: from the red spot on its mother's beak that the newly hatched sea gull taps on so that she will feed it [109] to the different facial expressions of chimpanzees that, according to Van Hoff [110] can be interpreted as equivalent to smiles, laughter or expressions of hatred. It is legitimate to think that in the case of humans, an abundant repertory of expressive forms is spontaneously developed during childhood. These forms are produced and recognized, especially in the non-verbal communication that a child establishes with his or her mother or with other children [111]. Many of these forms can be found in various cultures, such as elementary geometric shapes, basic colors and typical facial expressions of the main emotional reactions [112]. Painters have drawn widely from this repertory in order to express grief in the face of death, motherly love, suffering under torture, carnal love and ecstasy in diverse cultural contexts. Both the painter and the viewer react emotionally to memes of this type, which contributes to their selection as means of intersubjective non-verbal communication.

The systematic use of these prototypes with a strong emotional charge has limits, however. One of the strongest limitations lies in what Kubler [113] calls aesthetic fatigue, which results from having seen something too often or too long. It is entirely possible that this phenomenon constitutes one of the artist's creative drives, since artists constantly try to escape from it by making conscious attempts to give personal touches to the objects they create [114], ceaselessly renewing forms, figures and themes within the space where their style has free rein. One of several neural hypotheses concerning aesthetic fatigue bears on the attention and more particularly on the "orientation reaction" [115] of humans and other highly evolved animals in the presence of surprising or new stimuli. One of the physiological reactions is that the head and eyes turn toward the source of stimulation. Randomly distributed neurons in the brain stem help to regulate these movements. When a surprising event is repeated, losing its unexpected character, the amplitude of the orientation reaction progressively lessens: "habituation" takes place. Only an unfamiliar stimulus will cause a new response and will bring about "dishabituation." The singularity of a work of art systematically dishabituates the viewer.

Like the emergence of writing, which is posterior to it, the invention of art is a cultural phenomenon that is not linked to a noticeable change in the predispositions of the brain of Homo sapiens. On the contrary, art exploits inborn predispositions, previously set in the genes in the course of paleontological history [116]. To the predispositions mentioned above must be added those of learning and memory, which, in children and adults alike, are necessary requirements for the development of any culture. These faculties take on particularly spectacular dimensions in humans and are grafted onto another faculty, which is equally fundamental, but not particular to the species. Gombrich has noted that "without the faculty . . . of recognizing invariants among different variations and of maintaining the structure of a stable universe in the midst of changing conditions, art could never have existed" [117]. This capacity is, in fact, a necessary condition for survival among the organisms that make use of it, beyond the movements of their heads and eyes, to situate themselves in relation to the outer world, identify their fellow men and hit their prey accurately. This faculty is based on the capacity of the brain (mentioned in the first part of this paper) to use physical clues from the outer world to reconstruct invariants of shape, color and "relationships" that enable it to have access to an understanding of the world and to bring pertinent action to bear on it.

Nicolas Humphrey based aesthetic preferences on the faculty that associates learning and recognition of invariants, the

predisposition of men and animals to carry out experiments through which they learn to classify objects in the world around them. . . . The beautiful structures in art and nature are those that undoubtedly facilitate the task of classification by presenting signs of "taxonomic" relations between things in a manner that is at once informative and easy to grasp [118].

This argument is based first of all on the help that any classification in the organization of sensorial experience can bring by introducing economy of means to the description of the world and thus reducing the "burden of thought." In addition, Humphrey argues that such a "vital" faculty must have evolved as a source of pleasure. To classify is both to regroup different species in one category and to separate one category from another. "Taxonomic pleasure" probably results, then, from the simultaneous perception of rhyme and novelty. Experimental psychology has shown that children are drawn to stimuli that are neither entirely new nor totally familiar, but that present minor variations in terms of the original [119]. A painting undoubtedly exploits this faculty, since it is "a visual poem built on rhyme and contrast between visual elements" [120].

Finally, the predisposition that makes art a production specific to the brain of Homo sapiens is the faculty not only of building an inner representation of the world—what J.Z. Young refers to as a model of the world [121] and mankind—but of anticipating the evolution of this model, elaborating hypotheses and testing them through the human brain's function of simulation [122]. "Unlocking" the prefrontal cortex—as Leroi-Gourhan has termed it [123] gives access to a Darwinian evolution of mental and cultural representations, which makes use of the neural structures of reason and allows for Schiller's "reconciliation of the laws of reason and the interests of the senses" [124].

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