The following two papers by David S. Thaler: **EVIDENCE FOR EXTRAORDINARY VISUAL ACUITY IN LEONARDO'S COMMENT ON A DRAGONFLY** and **SFUMATO IN LEONARDO'S PORTRAITS: OPTICAL AND PSYCHOPHYSICAL MECHANISMS** are "in press" chapters in a book. Please include this reference when discussing these papers. The book is to be published during the summer of 2020:

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EVIDENCE FOR EXTRAORDINARY VISUAL ACUITY IN LEONARDO'S COMMENT ON A DRAGONFLY

BY DAVID S. THALER

David Thaler made a single presentation during the colloquium, which spanned two subjects. It made more sense therefore to publish two papers in these proceedings.

Abstract

Leonardo da Vinci conveys images that "in real life" only occur for a moment. Two prominent biographers of Leonardo, Kenneth Clark and Walter Isaacson, agree on Leonardo's temporal acuity, however, they infer different causes and consequences. Clark invokes "supernormal... nerves of his eye and brain" whereas Isaacson asserts acts of will and universally cultivatable skills of observation and curiosity. The contrasting ideas of Clark and Isaacson echo debates of nature versus nurture. Contemporary analysis shows cases in which "both are right," e.g., a particular genotype might facilitate efficacious training. However, other cases support extremes of one or the other. This article does not resolve the issue of nature versus nurture with respect to Leonardo's quick eye. Instead, it takes the question as a starting point to ask two questions: (1) Is it possible to quantify Leonardo's "fast eye"? (2) If there were a DNA sequence contribution to Leonardo's "fast eye", what might it be? Regarding point 1, Leonardo's "fast eye" is reframed in psychophysical terms as a rapid flicker fusion frequency (FFF) and a quantitative estimation is attempted via his comment on the relative movement of front and rear wings of a dragonfly compared with modern measurements that use high-speed video. Regarding point 2, the hypothesis is proposed that if there is a DNA-sequence basis for a fast FFF, it will be found in as yet uncharacterized alleles of retinal-expressed genes important for determining the maximum FFF.

Leonardo's visual acuity: Nature or Nurture ?

Kenneth Clark in his 1939 biography [1] discussed Leonardo's visual acuity in the following terms: "This book is not concerned with Leonardo as an inventor, but his studies of birds have a bearing on his art because they prove the extraordinary quickness of his eye. There is no doubt that the nerves of his eye and brain, like those of certain famous athletes, were really supernormal, and in consequence he was able to draw and describe movements of a bird which were not seen again until the invention of the slow-motion cinema" [1].

Clark elaborated on his interpretation that Leonardo's eyes and their neural processing components were innately operating above the normal human range:

Certain things in his art are clear and definable; for example, his passionate curiosity into the secrets of nature, and the inhumanly sharp eye with which he penetrated them—followed the movements of birds or of a wave, understood the structure of a seed-pod or a skull, noted down the most trivial gesture or most evasive glance [1].

His super-human quickness of eye has allowed him to fasten on the decorative aspects of the subject, since confirmed by spark photography, and we must take these drawings of water as genuinely scientific [1].

Clark quoted Leonardo directly to demonstrate the artist's self-awareness of what would now be called the psychophysics of visual acuity, in this case with respect to afterimages: "A stone falling through the air leaves on the eye which sees it the impression of its motion, and the same effect is produced by the drops of water which fall from clouds" [1] .

...the general effect is one of a graceful speed and of a hunter's certainty of eye [1].

A rendering of nature complete and learned enough to satisfy his interest in its function seemed to involve the idea of finish, and his own preternatural sharpness of eye tempted him in the same direction [1].

A masterpiece of this kind is the study of a Star of Bethlehem among swirling grasses which … combines the rhythmic movement of his hand with the microscopic

steadiness of his eye, so that it becomes an essential token of his art when freed from all conscious intuitions, dramatic or professional [1].

Walter Isaacson in his 2017 biography, disagrees with Clark's interpretation of Leonardo's visual acuity:

Kenneth Clark referred to Leonardo's "inhumanly sharp eye." It's a nice phrase, but misleading. Leonardo was human. The acuteness of his observational skill was not some superpower he possessed. Instead, it was the product of his own effort. That's important, because it means that we can, if we wish, not just marvel at him but try to learn from him by pushing ourselves to look at things more curiously and intensely [2].

A book review asserts that Isaacson succumbs to the self-help of "TED-ism" [3]. The review itself seems to take a hereditarian position "...Leonardo da Vinci was born with extra bundles of receptors, attuned to frequencies his peers could not hear and capable of making connections no one else could see... " I believe that this criticism of Isaacson, at least as it concerns visual acuity, is ungenerous. Isaacson may or may not be wrong. But even if Isaacson is wrong, it may be in an interesting way. Whether Leonardo's eye is or is not unusual in a biological sense remains unsettled. It is a good question because of its potential to be rigorously framed and for its implications to be investigated by experiment. Rhetoric alone cannot settle the matter. Here we offer a more detailed analysis of the components of vision, consider the extent to which it is possible to infer them from the works of Leonardo, and suggest a research program to explore variation in human abilities, including their further reaches.

Toward the farther reaches of human nature

One approach to extraordinary work is to ask if it was carried out by a person who is meaningfully different in a biological sense. There is a fairly extensive literature of speculation regarding visual pathologies that may have afflicted Leonardo. A related literature considers possible pathologies in the subjects of some of his portraits. This literature on various named pathologies will not be reviewed here. Instead, we focus on the idea that there may be "counter-pathologies," i.e., optimum states that in some cases are as different from the norm as are pathologies. Because of a medical orientation and desire to help the afflicted on the part of many researchers, physician-researchers, and sources of their funding, optimum states have not been as explored as have pathologies. Psychologist Abraham Maslow, in his book 'The Farther reaches of human nature' cautioned against a narrow focus on pathology and advocated a different orientation that studies individuals who function at the highest levels [4]. This article follows Maslow's lead but brings it into the level of sensory apprehension and processing rather than issues concerning mental and emotional health.

A related follow-up is to ask if DNA sequence might help interpret the work or the person who created it. The question here becomes "Might there be a particular DNA sequence or set of DNA sequences that contribute to Leonardo's genius?" A few of the premises, contexts, and consequences of this question are discussed below.

Leonardo da Vinci possessed extraordinary visual acuity in artistic and intellectual senses. This statement allows the question of whether he possessed "extraordinary visual acuity" in a biological sense. Parsing the attributes of visual acuity is preliminary to seeking its sources in DNA sequences or elsewhere. What exactly does the phrase "extraordinary visual acuity" mean?

Three domains of visual acuity

For this analysis, we separate vision into three domains: spatial, spectral, and temporal. We explore each domain to ask if elements of Leonardo's work suggest he had "extraordinary acuity" in that domain. A complicating factor is that when these domains are examined experimentally, none are truly independent. The interdependence of variables preclude certainty regarding Leonardo. The uncertainties also suggest directions for psychophysical, art historical, and artistic research. From the analysis and review summarized below, the strongest — though very far from definitive — case for extraordinary perception by Leonardo can be made for the temporal aspects of his vision.

Spatial acuity. The spatial aspect of vision is expressed as resolution, i.e., how close two objects can be and still be correctly perceived as separate. Spatial resolution at a given distance is what a standard eye chart exam measures (please read the letters on the second row from the bottom). Twenty-twenty vision means that at six meters, i.e., about 20 feet, contours approximately 1.75 millimeters apart can be distinguished. The maximum spatial resolution at close range for most humans is between 50-100 microns, in the range of diameters of a single human hair. The distance of the smallest in-focus distinction depends on how close an eye can focus. If focused at 12 inches (30.5 cm), then the smallest possible is 85 microns. If the focus can be brought closer, the theoretical possibility is to see smaller detail.

"Extraordinary visual acuity" in the spatial realm implies an ability beyond the average person to see small things or to distinguish separate objects that are close. Leonardo da Vinci created drawings with fine visual detail. Italian physicist Cesare Marchetti, who has deeply studied the works of Leonardo and given great attention to the scale of their fine-detail, remarks that "Leonardo had an eagle eye and could go beyond the skills of the best Florence miniaturists of the time, who incidentally were his friends and neighbors. I would say his limit was in the range of a tenth of millimeter" [5]. Comparing Marchetti's estimate with contemporary norms yields scant evidence that Leonardo possessed spatial resolution beyond the ordinary.

However, Marchetti based his estimate of a limit of 100 microns (a tenth of a millimeter) on what Leonardo made. It seems likely that what Leonardo was able to see with his eyes and mind was smaller than what he was able to render with his tools and hands. Therefore, the statement of "about a tenth of a millimeter" must be taken as an upper limit, since he must have seen at least, and most likely saw better, than the spatial resolution at which he created. The neurobiology of eye-hand coordination is an area of ongoing research with many unknowns [6].

Spectral acuity. The meaning of spectral acuity also requires further interpretation even at the most elementary level. "Spectral acuity" might mean how well one can distinguish pure, i.e., single wavelengths of light. Each primary color is a specific wavelength band of light, secondary colors being the simultaneous presentation of different primary colors. In a related sense, "spectral acuity" might mean how close two wavelengths of light can still be distinguished.

Another possible interpretation for "extraordinary spectral acuity" would be an extended visual range in wavelength. A person with normal vision can discern a spectral range of 400-700 nanometers (nm). Many animals have a different spectral range of vision than humans. Some are able to see light in the infrared range with wavelengths longer than 700 nm, and some in the ultraviolet at wavelengths shorter than 400 nm. Some snakes [7], insects [8], and fish [9] have infrared vision and many animals see into the ultraviolet [10].

Vision occurs by means of visual pigments in the eye, where each pigment has a specific absorption spectrum. When a pigment absorbs light, it begins a signaling cascade. The visual pigments themselves are relatively well understood. The protein moiety of visual pigments, opsins, are encoded by genes. The amino acid sequence of the various opsin genes and alleles is largely determinative of their spectral properties. The amino acid sequence and hence the spectral properties of opsins are encoded in their DNA sequence. Different alleles of opsin genes or unusual combinations of opsin genes can lead to altered spectral properties in vision.

Either enhanced spectral differentiation within the normal human range of 400-700 nm or an enhanced spectral range, below 400 nm or above 700 nm, could be mediated by an allele of an opsin encoding an unusual pigment. A different way to get altered spectral properties through the opsin genes would be to have a greater repertoire of genes or alleles expressed in the same organism. Most humans express three rhodopsin pigments whose absorption peaks are determined by the opsin genes. However, occasionally four spectrally distinct opsins are expressed, producing a condition called tetrachromacy. Individuals with this rare condition might have enhanced color discrimination [11, 12].

Different opsin genes underlie the different spectral ranges of vision observed among various animal species. It is conceivable that Leonardo had either a rare allele of an opsin gene, or perhaps a rare combination of visual pigments. And it is conceivable that insight into these matters could be gained by examination of Leonardo's DNA sequence.

Although an altered opsin would contribute to seeing colors with more discrimination, or seeing wavelengths that are invisible to most people, there is to my knowledge no specific reason to support this conjecture for Leonardo da Vinci. The insightful study of Cesare Marchetti on spatial resolution is apparently not matched in the realm of spectral characteristics.

Humans can enhance their visual capabilities through prosthetics such as night vision goggles or infrared imagers and extend their senses in part through the techniques of augmented reality. Genetic engineering offers potential to enhance spectral discrimination and range. Dragonflies have up to 30 opsin pigments with a wide range of properties [13]. Replacement of a mouse opsin gene with a human gene is reported to confer new chromatic discrimination [14] although, the tests used to document the new spectrally-dependent behavior have been challenged [15]. Stable introduction of an extra opsin repairs a mouse model of opsin deficiency [16]. Whether the new perception comes from sensory enhancement by external (e.g., electronic) means or by introducing new genes, the human nervous system is able to usefully integrate additional visual information [17].

Temporal acuity. "Temporal acuity" can mean how close in time two events can occur and still be distinguished as separate. This meaning of temporal acuity in vision partially overlaps with the better-defined psychophysical parameter flicker fusion frequency (FFF), sometimes called critical flicker fusion frequence (CFFF). The CFFF is often defined as the rate above which a white LED flashing on and off in a darkened room is seen as continuously on [18]. Measured in this way, the range of FFF in normal humans varies from about 20 to a little over 40 flashes per second, expressed in hertz (Hz). The flicker fusion frequency of the most perceptive in this case is less than 50 Hz. This agrees with the 48 or 72 frames-per-second rate of most current motion pictures.[30]

Evidence that Leonardo da Vinci may have had extraordinary acuity in the temporal aspect of vision seems stronger than for enhanced spatial or spectral acuity. Consider Leonardo's observation on the flight of dragonflies as reported by Isaacson [2]:

"The dragonfly flies with four wings, and when those in front are raised those behind are lowered" [2].

Isaacson reports this observation on dragonflies in flight on the same page as Leonardo's advice that each of us can become a more acute observer through practice.[31]

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[30] Contemporary motion pictures appear to be in smooth, continuous movement because images are presented to the eye at rates that exceed the critical flicker fusion frequency. "Flicks," the American slang term for motion pictures, originated with the slower frame rates used in early movies, in which the flickering was visible to many (but not all) viewers. The "flickering rate" is sometimes different than the rate at which successive different images are presented. In some formats the same still image is presented more than one time. For example, in some formats different images are given 24 times per second but each image is presented twice so that the flicker rate is 48Hz.

[31] The author's informal investigation of dragonflies in Europe and Western Canada during the summers of 2018 and 2019 found Isaacson's guidance aspirational but not attainable. One colleague reported that he saw the out of phase wings for a few moments during one observation but never before or since, despite numerous tries. "Sight," the first episode of the informative and wonderfully produced BBC video miniseries *Super Senses: The secret Power of Animals,* shows dragonfly flight in slow motion and also the visual parameters of flicker fusion frequency needed to see it in real time ["How Do Dragonflies See the World?" Animal Super Senses, BBC, 20 November 2015, 4 minutes 13 seconds, youtu.be/m5XUdvBO_TE] .

The wingbeats and coordination of the front and back wings of dragonflies have been the subject of intensive study using high-speed cameras. It is possible to compare these data with Leonardo's observation to estimate the temporal acuity needed to make his correct observation of the relative movement of their front and back wings (see Figure 147).

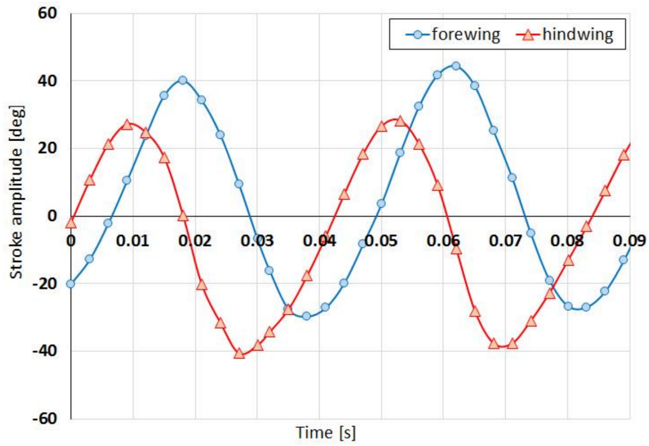

Figure 147: Kinematic study of dragonfly wingbeats shows a full repeat frequency of about 25 per second and a phase difference of about 10 milliseconds between forewings and hindwings. The maximum angle between the wings is 40-50 degrees. The cycle difference between the front and rear wings is 10/40 or ¼ of cycle which if plotted on a circle would correspond to a 90 degree phase shift but what the eye has to observe is the smaller actual angle between front and rear wings which never goes beyond 50 degrees (see x-axis position 0.07 on Figure 1).

Source: Figure 7 from reference [19]; see also reference 21.

The wingbeat frequency can be read from the peak-to-peak distance of the sinusoidal wave in Figure 1. It is about 40 milliseconds (ms) (Figure 1, first peak ~20ms, second peak ~60ms), which corresponds to about 25 complete-cycle wingbeats per second. Figure 1 also shows that the hindwings and forewings are not perfectly inverse in their phase relationships but rather that their phases are offset by approximately one quarter of a cycle. The forewings and hindwings are displaced by approximately 10 ms. Ten milliseconds, or one-hundredth of a second, corresponds to a flicker fusion frequency of 100 Hz, approximately twice the fastest flicker fusion frequency, as conventionally measured, for humans. The wingbeat frequency and phase relationships of dragonfly wings are active subjects of contemporary research [20-22]. Present-day interest in dragonflies shares some of Leonardo's motivation: to make flying machines. Currently the stated interests are in small drones that can maneuver well in tight spaces such as inside buildings.

Cautions in attributing an extraordinary flicker fusion frequency to Leonardo

The critical flicker fusion frequency is highly dependent on experimental conditions under which it is measured. The measure of white light flickering in a darkened room gives a number that works fairly well and is repeatable although not universal [23, 24].

Other measures yield different numbers. The perception of motion and of change in vision depends very much on how it is presented. A different experimental protocol where high-contrast images in black and white are alternately flipped allows humans to perceive flicker at an average of 500 Hz, with one out of ten tested individuals perceiving the flicker at 1000 Hz [25]. With the simple white light flashing on and off, the range of human perception is approximately 20 Hz, meaning that slow perceivers have an FFF of about 20 Hz and the fast perceivers about 44 Hz. With the screen test, the difference between slow and fast perceivers is approximately 700 Hz, i.e., between 300 Hz and 1000 Hz. Ambient light, contrast, and colors all affect the FFF, and there is individual variation in the effects of these variables. An additional variable is that the apparatus and methods to measure FFF tend to be specific to each laboratory. The numbers arrived at by different groups may be difficult to compare despite having the same name of FFF.

Isaacson quotes Leonardo's notebooks as detailing special efforts required to correctly perceive the alternating wings of a dragonfly. These may have included not only the presence of the insects but also conditions of light, contrast, and observer attention. Critical flicker fusion frequency can be improved by training [26], although there is controversy about the efficacy of particular methods. General cognitive benefits of training for increased critical FFF have been suggested but not convincingly demonstrated [27]. Physiological state such as fatigue and pharmacology reversibly change FFF [28].

Possible genetic contributions to critical flicker fusion frequency

At this writing it is unknown whether there is a genetic contribution to FFF variation among humans.

Animal species differ in many aspects of their vision, including differences in FFF [29]. Species of insects and birds have been reported with especially high CFFFs (see Figure 148).

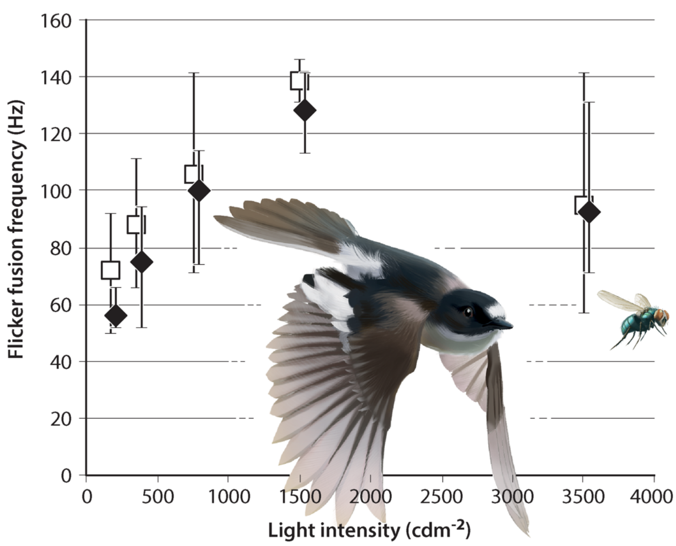

Figure 148 : Ultra-rapid vision in birds. This measurement of flicker fusion frequency (in hertz) at moderate light intensity (in candles per square meter) shows a maximum of 141 Hz for collared flycatchers (solid diamonds) and up to 146 Hz for pied flycatchers (open squares).

Source: Figure 2 from reference 31.

Reference 31 includes the following 1-minute video clip showing two flies in flight, first at the speed perceived by humans and then at the slower speed that might be perceived by flycatchers: Interpretation of what the bird sees when chasing flies.

There is a literature based on several different methods of measurement that describes such animals as living in a "slow-motion world" [30]. The reasoning behind this vocabulary is notably subjective for the scientific literature. One way that the effects of a high FFF are represented is by making a high-frame-rate movie of the subject of interest and then playing it back at a slower frame rate but one that is still above the CFFF of the human observer. For example, if an activity is filmed at a frame rate of 1000 images per second and played back at a rate of 50 frames per second, then one second in real time will take 20 seconds in playback. This gives human viewers the impression of "slow motion." It is not known if the subjective experience of an animal or a human with a high CFFF is akin to that represented by slow-motion video. People commonly report intense experiences such as car accidents felt as if they were occurring in slow motion. Such observations have been difficult to repeat under controlled laboratory conditions, and it may be that the recollection rather than the experience itself was in fine-grained, high resolution, which apparently enhanced "slow-motion" detail [31-33].

The characteristics of vision are not constants in the same way as the force of gravity, the number of molecules in a mole, or the speed of light. The quantitative results of psychophysics experiments are often not robust against small variations in experimental design and are not necessarily continuous. For example, the intensity and spectrum of light, subject fatigue, pharmacology, and habituation all may have strong and discontinuous effects.

The physiological, genetic, and molecular-mechanistic basis of FFF and its quantitive variation, either among species or among individuals within a species, are unknown. However, there are reasonable hypotheses. Comparative studies of Diptera (winged flies) find that the FFF varies by more than an order of magnitude for different species within the order (Diptera is a large order estimated to contain a million species of which approximately 125,000 have been partially characterized). Potassium (K+) channels expressed in retinal cone cells of Diptera have properties that correlate with species-specific FFF [34, 35]. In mammals the KCNB1 and KCNV2 K+ channel genes are expressed in the retina, and certain altered alleles in these genes are known to cause visual defects in mouse models and in humans [36]. I hypothesize that as yet unknown or uncharacterized alleles of cone-expressed K+ channels underlie FFF variation among individuals within the same species, and will be found as one component of human FFF variation.

Freezing an instant of motion and flicker fusion frequency

Careful observers have noted that Leonardo was deeply concerned with the representation of movement [37]. Freezing a moment in movement seems critical to his representation of the flight of birds, springy hair, the movement of limbs, and swirls of water. Motion that at a slower FFF would appear a blur, with a sufficiently fast FFF will be distinct. A fast FFF may have contributed to Leonardo's remarkable ability to represent critical instants in continuous movement. This "freeze frame" representation was remarked upon by Isaacson with reference to *The Last Supper* [2, pp. 281-282]. Isaacson was himself discussing and contrasting his reaction to the fresco with reference to Kenneth Clark's previous critique of Leonardo's "snapshot" representation of a momentary interaction between Christ and the apostles.

Leonardo is not alone in artistic evidence suggesting a fast flicker fusion frequency and freeze frame memory

The equally or more famous (in Japan) artist Katsushika Hokusai (1760-1849) created a woodblock print of a mayfly (a dragonfly relative) whose flight characteristics resemble those of a dragonfly (see Figure 149).

Figure 149 : Katsushika Hokusai's Bellflower and Dragonfly.

Source: Wikimedia Commons

The front and back wings of Hokusai's mayfly are out of phase but not by 180 degrees as implied by Isaacson's quote from Leonardo's notebooks. The modern slow-motion analysis of dragonflies shows that the front and back wings are often out of phase by about 40 degrees (see Figure 1), which is consistent with Hokusai's masterful portrayal.

Hokusai's most famous painting, at least in the Western world, *Great Wave off Kanagawa*, also manifests frozen motion (Figure 150).

Figure 150 : Katsushika Hokusai's Great Wave off Kanagawa.

Source: Wikimedia Commons

Mona Lisa's smile has been the subject of intense analysis and it may be audacious to make an additional remark with respect to it. Elaine Scarry describes how it is normally easier to remember the face of a person who is smiling than to picture a face that is breaking into a smile: "To understand the meaning of the words 'So and so smiled' is effortless; but actually to have the image of a person's face break into a smile … is extraordinary. Tolstoy tells us at the opening of *Anna Karenin* that Levin can make a perfect image of Kitty in his mind but cannot get the image to smile (thus he is always floored when he meets Kitty in person)" [38]. An aspect of the enigmatic nature of *Mona Lisa*'s smile may be that it is not a smile being held but the transient moment of a smile being formed. Perhaps Leonardo was able to apprehend Lisa's smile effectively in slow motion and thereby capture the most meaningful transients of movement.

Thoughts and caveats regarding research potentials

Leonardo's copious notes on bird flight have potential for exploration in a manner similar to recent dragonfly analyses [20-23]. Slow-motion studies of bird flight could be quantitatively compared with Leonardo's observations. Of particular value might be comparing Leonardo's statements concerning the relative times of upstroke versus downstroke in the wingbeat of various bird species with measurements derived from contemporary high-speed imaging and analysis ([39] and later papers that cite this 1996 work). High-frame-rate analysis of the upstroke and downstroke of the wingbeat of birds similar to those Leonardo da Vinci studied may allow further estimation of his FFF in this context. Coupled contemporary psychophysical studies would also be possible. These studies would allow determination of optimal conditions for observation. They would also allow exploring the potential for training to increase frame-rate perception.

There is a likely genetic contribution to variations in FFF among species. These differences could be the subject of comparative genomics research. The same genes or genetic networks may or may not be responsible for the variation in FFF among individuals within the same species. As a research program, one could imagine screens or selections in drosophila or zebrafish, for example, for mutants with altered FFF. The possibilities of training as well as genetics could be explored in model systems. The contributions of each will plausibly turn out to vary in interesting ways depending on the species. Candidate genes and genetic networks uncovered in other species and model systems could be tested in a targeted way in humans.

Differences in critical flicker fusion frequency between species and individuals within the same species may, or may not, turn out to have similar causation. The study of both questions should be carried out in parallel because work on either question is likely to inform the other. Kenneth Clark's possibly prescient remark that "*There is no doubt that the nerves of his eye and brain, like those of certain famous athletes, were really supernormal…*" [1] suggests studies focused on athletes with demonstrably quick vision. Perhaps the clearest case is in American baseball because it is said that elite batters can see the seams on a pitched baseball. The ball rotates between 30 and 50 times a second. Depending on its orientation, either two or four symmetric seams are visible to the batter so that the stimulus would be presented between 60 and 200 times per second. The lower number is already above the highest normal CFFF as measured in standard ways by an LED in a dark room. Do elite baseball players notice the flicker in 48 frames-per-second films? Here we give links to two excellent YouTube videos on spin in baseball that alternate slow-motion with real-time views:

MLB Crazy Spin Rates, 3 mn 30 sec, Highlight Reel, youtu.be/wWNKDKkslUo

Bill's Blackboard: What Is Spin Rate? 3 mn 47 sec, MLB Network, youtu.be/OX90_TQr5EI

Genome-wide association studies (GWAS) among humans with high CFFF might be of interest, as would other approaches to genetic analysis, such as studies of families and other related groups.

Areas of inquiry include the potential for training to increase FFF, including questions of whether it can be learned, how, and if it is a "one size fits all" education paradigm. Whether or not a higher FFF is of wider or general benefit is uncertain. There is a possibility that FFF is a "gateway" to enhanced ability in many realms, including art and science. Pilots and pilot trainers may value a high critical FFF, but they are not immune to errors in the evaluation and optimization of psychophysical skills [40].

One argument against a genetic contribution to Leonardo's genius is the absence of evidence for talent in any of his relatives. Two contravening possibilities deserve consideration. The first is that a "Leonardo phenotype" might require the conjunction of alleles at several loci such that the presence of an incomplete set has no effect. This line of reasoning is well developed as quantitative genetics and epistasis in the context of population biology (which is not to say it necessarily applies to this case, simply that it is logically possible). A second line of reasoning is that the genius effect in Leonardo could involve a *de novo* mutation in the germ cells that gave rise to the embryo or perhaps during post-zygotic development. It is becoming clear that *de novo* mutations play a larger-than-previously-anticipated role in several phenotypes including susceptibility to infectious diseases [41] and autism [42]. There is no specific evidence to support the hypothesis that *de novo* mutation applies to Leonardo's singular case. However, both the conjunction of alleles and the *de novo* mutation hypotheses could conceivably gain unique support from the analysis of Leonardo's DNA sequence. We know of no other way to directly address these hypotheses.

I return to the first paragraph of Kenneth Clark's 1939 book before posing my own slight disagreement with him through remarks that should be considered as an extension and homage. Clark wrote:

This book is concerned with the development of Leonardo da Vinci as an artist. His scientific and theoretical writings can only be studied intelligently by those who have a specialized knowledge of medieval and Renaissance thought. His art, and the personality it reveals, is of universal interest, and like all great art should be re-interpreted for each generation [1].

Leonardo's science can also be re-read and reinterpreted for each generation. Such reexamination is necessary not only for its significance in history, e.g., to make the point that the study of anatomy would have advanced by decades, or even centuries, if only Leonardo had published [43]. Not only from the point of view of comparing Leonardo to other thinkers and artists, valuable as these approaches are. Leonardo's works can also be studied now and into the future by practicing scientists for inspiration, good questions, and research ideas. To study Leonardo means not only that Leonardo is the subject of investigation. It also means to continue asking questions he asked but using methods of thought and instruments available today, an approach foreshadowed by Martin Kemp more than 40 years ago[32]:

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[32] A difference with Kemp's likely meaning is worth articulating with respect to forward-looking research on perception and consciousness. "Representation" in Kemp's use may refer to

In our eyes, no less than Leonardo's, the relationship between representation and perception certainly cannot be regarded as a dead issue [44].

Acknowledgments

This manuscript evolved from talks given at meetings of the Leonardo da Vinci DNA project held in Florence (May 2018), in Madrid (May 2019), as well as the International Symposium: *Léonard de Vinci, Anatomiste. Pionnier de l'Anatomie comparée, de la Biomécanique, de la Bionique et de la Physiognomonie*, held in Amboise in October 2019. Jesse Ausubel invited me to consider biological hypotheses that could be relevant to Leonardo da Vinci's genius. Kenji Adzuma pointed out the remarkable temporal acuity inferred by the work of Katsushika Hokusai and the role of fast eyes in baseball. Phil Richardson helped in observing dragonflies. Alexander Borst and Aguan Wei generously shared their profound insights into molecular mechanisms of vision. Csba Helfer, Huihe Qiu and Wie Shyy gave kind permission to include their figure on dragonfly wing motion. Dale Langford's incisive editing redacted and thereby improved the final manuscript. Thanks for encouragement and insight to the above and Fiona Doetsch, Karl Doetsch, Christian Galvez, Ross King, Caroline Lemerle, Henry de Lumley, Marguerite Mangin, Angelo Pontecorboli, Amalie R. Rothschild, Saad Shaikh, CW Tyler, Yunke Wang. I dedicate this manuscript to Franklin W. Stahl on the occasion of his 90th birthday.

References

1. Clark K: **Leonardo da Vinci: An Account of His Development as an Artist**. Bentley House, London: Cambridge University Press; 1939.

2. Isaacson W: **Leonardo da Vinci: The Biography**. London: Simon & Schuster; 2017.

3. Senior J: "**Portrait of a True Renaissance Man,**" *New York Times,* 1 November 2017.

4. Maslow AH: **The Farther Reaches of Human Nature.** Penguin; 1993.

5. **Marchetti, C. Leonardo had an eagle eye** [http://www.cesaremarchetti.org/leonardo_2.php]

6. Mooshagian E, Snyder LH: **Spatial eye-hand coordination during bimanual reaching is not systematically coded in either LIP or PRR**. *Proceedings of the National Academy of Sciences of the United States of America* 2018, **115**(16):E3817-E3826.

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manifested art viewed as a product separated from its creator or it may refer to a system of abstraction as in a geometrical representation of perspective. "Representation" in neurobiology and consciousness research includes neural representations of perception. By hypothesis, as understanding improves, there will be less and less separation between "perception", its neural-consciousness meaning as "representation" and action (a direction toward this future is articulated by Zdravko Radman in 'The hand, an organ of the mind' MIT press, 2013 and a video 'Thinking with the hands' https://youtu.be/yme3qhlYGlk).

7. Grace MS, Woodward OM, Church DR, Calisch G: **Prey targeting by the infrared-imaging snake Python molurus: effects of experimental and congenital visual deprivation**. *Behav Brain Res* 2001, **119**(1):23-31.

8. Klocke D, Schmitz A, Soltner H, Bousack H, Schmitz H: **Infrared receptors in pyrophilous ("fire loving") insects as model for new un-cooled infrared sensors**. *Beilstein J Nanotechnol* 2011, **2**:186-197.

9. Gallego B, Verdu JR, Carrascal LM, Lobo JM: **A protocol for analysing thermal stress in insects using infrared thermography**. *J Therm Biol* 2016, **56**:113-121.

10. Cronin TW, Bok MJ: **Photoreception and vision in the ultraviolet**. *J Exp Biol* 2016, **219**(Pt 18):2790-2801.

11. Jordan G, Mollon JD: **A study of women heterozygous for colour deficiencies**. *Vision Res* 1993, **33**(11):1495-1508.

12. Jameson K, Winkler A, Goldfarb K: **Art, interpersonal comparisons of color experience, and potential tetrachromacy**. In: *IS&T International Symposium on Electronic Imaging Technical Session on Human Vision and Electronic Imaging: 2016*; 2016.

13. Futahashi R, Kawahara-Miki R, Kinoshita M, Yoshitake K, Yajima S, Arikawa K, Fukatsu T: **Extraordinary diversity of visual opsin genes in dragonflies**. *Proceedings of the National Academy of Sciences of the United States of America* 2015, **112**(11):E1247-1256.

14. Jacobs GH, Williams GA, Cahill H, Nathans J: **Emergence of novel color vision in mice engineered to express a human cone photopigment**. *Science* 2007, **315**(5819):1723-1725.

15. Makous W: **Comment on "Emergence of novel color vision in mice engineered to express a human cone photopigment."** *Science* 2007, **318**(5848):196; author reply 196.

16. Zhang Y, Deng WT, Du W, Zhu P, Li J, Xu F, Sun J, Gerstner CD, Baehr W, Boye SL *et al*: **Gene-based Therapy in a Mouse Model of Blue Cone Monochromacy**. *Sci Rep* 2017, **7**(1):6690.

17. Gundlach BS, Frising M, Shahsafi A, Vershbow G, Wan C, Salman J, Rokers B, Lessard L, Kats MA: **Design considerations for the enhancement of human color vision by breaking binocular redundancy**. *Sci Rep* 2018, **8**(1):11971.

18. Eisen-Enosh A, Farah N, Burgansky-Eliash Z, Polat U, Mandel Y: **Evaluation of critical flicker-fusion frequency measurement methods for the investigation of visual temporal resolution**. *Sci Rep* 2017, **7**(1):15621.

19. Hefler C, Qiu H, Shyy W: **Dragonflies utilize flapping wings' phasing and spanwise characteristics to achieve aerodynamic performance**. *arXiv:161205353v1* 2016.

20. May M: **Dependence of flight behavior and heat production on air temperature in the green darner dragonfly Anax junius (Odonata: Aeshnidae)**. *J Exp Biol* 1995, **198**(Pt 11):2385-2392.

21. Hefler C, Qiu H, Shyy W: **Aerodynamic characteristics along the wing span of a dragonfly Pantala Flavescens**. *J Exp Biol* 2018.

22. Li Q, Zheng M, Pan T, Su G: **Experimental and numerical investigation on dragonfly wing and body motion during voluntary take-off**. *Sci Rep* 2018, **8**(1):1011.

23. Van Haute L, Powell CA, Minczuk M: **Dealing with an unconventional genetic code in mitochondria: The biogenesis and pathogenic defects of the 5-formylcytosine modification in mitochondrial tRNA(Met)**. *Biomolecules* 2017, **7**(1).

24. Zahonova K, Kostygov AY, Sevcikova T, Yurchenko V, Elias M: **An unprecedented non-canonical nuclear genetic code with all three termination codons reassigned as sense codons**. *Curr Biol* 2016, **26**(17):2364-2369.

25. Davis J, Hsieh YH, Lee HC: **Humans perceive flicker artifacts at 500 Hz**. *Sci Rep* 2015, **5**:7861.

26. Zhou T, Nanez JE, Sr., Zimmerman D, Holloway SR, Seitz A: **Two visual training paradigms associated with enhanced critical flicker fusion threshold**. *Front Psychol* 2016, **7**:1597.

27. Seitz AR: **A new framework of design and continuous evaluation to improve brain training**. *J Cogn Enhanc* 2018, **2**(1):78-87.

28. Garcia-Gea C, Martinez J, Ballester MR, Gich I, Valiente R, Antonijoan RM: **Psychomotor and subjective effects of bilastine, hydroxyzine, and cetirizine, in combination with alcohol: a randomized, double-blind, crossover, and positive-controlled and placebo-controlled Phase I clinical trials**. *Hum Psychopharmacol* 2014, **29**(2):120-132.

29. Schaeffel F: **[Comparative analysis of light sensitivity, depth and motion perception in animals and humans]**. *Ophthalmologe* 2017, **114**(11):997-1007.

30. Reas E: **Small animals live in a slow-motion world**. *Sci Am* 2014.

31. Nyman TJ, Karlsson EPA, Antfolk J: **As time passes by: Observed motion-speed and psychological time during video playback**. *PLoS One* 2017, **12**(6):e0177855.

32. Stetson C, Fiesta MP, Eagleman DM: **Does time really slow down during a frightening event?** *PLoS One* 2007, **2**(12):e1295.

33. Tse PU, Intriligator J, Rivest J, Cavanagh P: **Attention and the subjective expansion of time**. *Percept Psychophys* 2004, **66**(7):1171-1189.

34. Heras FJ, Anderson J, Laughlin SB, Niven JE: **Voltage-dependent K(+) channels improve the energy efficiency of signalling in blowfly photoreceptors**. *J R Soc Interface* 2017, **14**(129).

35. Laughlin SB, Weckstrom M: **Fast and slow photoreceptors- a comparative study of the functional diversity of coding and conductances in the Diptera**. *J Comp Physiol A* 1993, **172**:593-560.

36. Hart NS, Mountford JK, Voigt V, Fuller-Carter P, Barth M, Nerbonne JM, Hunt DM, Carvalho LS: **The role of the voltage-gated potassium channel proteins Kv8.2 and Kv2.1 in vision and retinal disease: Insights from the study of mouse gene knock-out mutations**. *eNeuro* 2019, **6**(1).

37. de Lumley H, de Lumley M-A, Clarac F, Figarella J, Lamy P: **Leonardo da Vinci. Pioneer of comparative anatomy, biomechanics and physiognomy**. *International Journal of Anthropology* 2017, **32**:3-76.

38. Scarry E: **Dreaming by the Book**: Farrar Straus & Giroux; 1999.

39. Tobalske B: **Scaling of muscle composition, wing morphology, and intermittent flight behavior in woodpeckers**. *The Auk* 1996, **113**:151-177.

40. Kahneman D: **Thinking Fast and Slow**: Farrar, Straus & Giroux; 2011.

41. Alcais A, Quintana-Murci L, Thaler DS, Schurr E, Abel L, Casanova JL: **Life-threatening infectious diseases of childhood: Single-gene inborn errors of immunity?** *Annals of the New York Academy of Sciences* 2010, **1214**:18-33.

42. Alonso-Gonzalez A, Rodriguez-Fontenla C, Carracedo A: **De novo mutations (DNMs) in autism spectrum disorder (ASD): Pathway and network analysis**. *Front Genet* 2018, **9**:406.

43. Nuland S: **Leonardo da Vinci**. Penguin/Viking 2000.

44. Kemp M: **Leonardo and the visual pyramid**. *Journal of the Warburg and Courtauld Institutes* 1977, **40**:128-149.

20

SFUMATO IN LEONARDO'S PORTRAITS: OPTICAL AND PSYCHOPHYSICAL MECHANISMS

PAR DAVID S. THALER

Abstract

This paper considers physical and psychophysical mechanisms that Leonardo da Vinci did not define but which, by hypothesis, underlie his use of sfumato in portraits. Sfumato occurs in Leonardo's portraits in two different ways: (1) where the degree of focus is a function of distance from the observer, but also (2) where sharpness of focus differs among objects at the same or nearly the same distance. The proposed physical-optical mechanism for the first case follows from his advice to paint by overcast or evening light, when enlarged pupils decrease depth of field such that only a narrow band of distance is in focus at any one moment. A different mechanism is proposed to account for differences in sharpness between adjacent objects at an equal distance from the observer. With normal eye movement, the brain constructs a mental image integrating multiple instantaneous images, each of which had maximum clarity only in the small foveal region of the retina. This integration of multiple images is, by hypothesis, a mental construct that uses neural mechanisms akin to flicker fusion frequency as described in the companion paper. Leonardo's "quick eye" may have allowed him to recognize instantaneous images and their partial focus. Alternatively, he may have held a steady gaze long enough to recognize differential acuity within a visual field held preternaturally still by concentration, awe, fear, or affection.

Leonardo da Vinci sought to understand optics and the relationship of optics to visual perception. Perspective and anatomy are the clearest cases where Leonardo articulates his evolving understanding with words and diagrams in his notebooks as well as with non-notebook drawings and paintings [1-5].

Leonardo's genius was not limited to what he explained with words and diagrams in his notebooks. Some of his artistic expressions seem beyond those for which he had conscious knowledge, a theory, or even a name [6][1].

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[1] As an intermediate example, Leonardo was aware of what are now called "motion streaks," an effect whose mechanism remains a subject of research 500 years later [7. Apthorp D, Schwarzkopf DS, Kaul C, Bahrami B, Alais D, Rees G: **Direct evidence for encoding of motion streaks in human visual cortex.** Proc Biol Sci 2013, 280(1752):20122339.], but chose not to use it in his own work. It is exceptional to be articulate concerning what is not understood. Kemp noted: "From 1508 onwards he was engrossed in studying the infinite variables of the visible world, its illusions, ambiguities, deceptions and fleeting subtleties – all of which disrupted the linear stability of artificial perspective. His later notes are full of beguiling and brilliant observations as he strove to pin down the elusive butterfly of natural appearances. Looking at revolving objects such as a spinning wheel and 'whirling fire-brand' he saw that 'although they move on the one spot, they do not . . . reveal themselves as they are in reality' but leave a continuously blurred image of their parts" [2, p. 330].

Several of Leonardo's uses of blur in different contexts and for different purposes have been masterfully elucidated by Kemp [2, 8]. Without reviewing those that have been characterized previously, here I propose new and related types of blur as integral to features of Leonardo's portraits. To the best of my knowledge, Leonardo's notebooks do not show that he was consciously aware of the effects discussed in this paper. They appear to fall into a realm different than his expression in notebook words or diagrams but, by hypothesis, are expressed within his painted portraits. One of the new blur effects is purely optical. Another is based on neural integration of a temporal series of retinal images. Yet another blur effect is evident in his apparent use of the differential resolution in different regions of the retina. A fourth, neuro-optical mechanism occurs only under certain levels of illumination where rods and cones are simultaneously engaged. This light level coincides exactly with that favored by Leonardo for portraits.

The optical effect of pupil size on sharpness of focus and depth of field

The purely optical effect is that sharpness of focus and depth of field depend on aperture size, i.e., the diameter of the round hole through which light passes as it moves from the outside world onto the sensing surface. In the human eye, the pupil is the round hole through which light passes on its way through the lens, then the vitreous humor that fills the eyeball, to ultimately fall upon photoreceptor cells arrayed on the retina. Human pupil size changes dynamically, on average, from about 2 mm to about 8 mm.

We can illustrate the optical consequences of changing pupil size with the help of a contemporary electromechanical eye whose physical-optical parameters approximate the human eye (fig. 151).

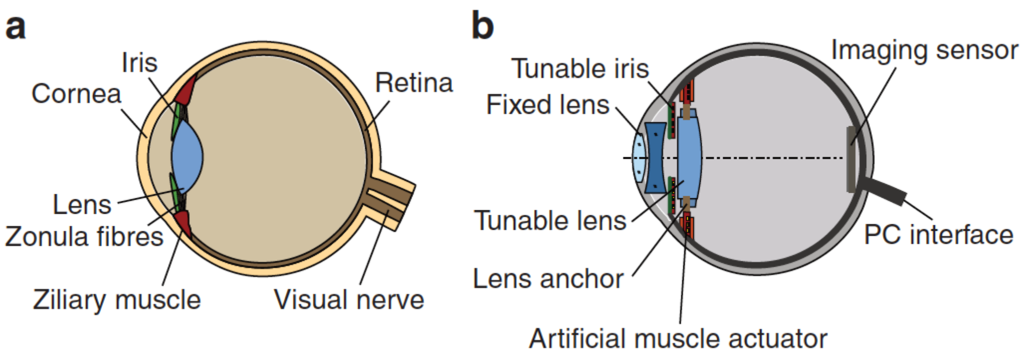


Figure 151: Cross sections of the human eye (a) and an engineered eyeball with a tunable imaging system (b). The optical image formed on the sensor at the back of the electro-mechanical eye is viewed on an external screen. The "tunable iris" of the electro-mechanical eye corresponds to iris of the human eye. The pupil is not labeled on these diagrams; it is the round opening (the hole in the donut) of the iris through which light passes.

Source: From Figure 1 reference 9.

Images taken with the electro-mechanical eye with different sizes of the tunable iris demonstrate the blur effect of seeing through a large-diameter pupil. Note two aspects of this blur effect: (1) The maximum sharpness of focus at the optimum focal plane, and (2) The depth of field, i.e., the distance in the Z-axis over which maximum focus does not noticeably degrade (Fig. 152).

Soft focus and shallow depth of field vs Sharp focus and deep depth of field

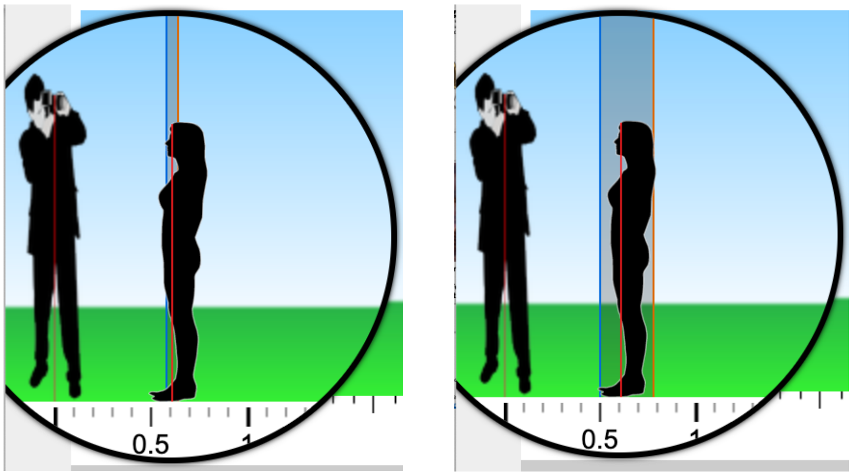
Pupil diameter 5.00 mm Pupil diameter 1.77 mm

Figure 152 : A scene imaged by the engineered eyeball with two different settings of the "tunable iris corresponding to different pupil sizes of the human eye. Distance between front and rear chess pieces is 220 mm.

Source: Figure 9 in reference 9.

The effects of aperture size on sharpness of focus and depth of field are core considerations for photographers and cinematographers.[2] The human eye is about 24 mm in diameter. In figure 153, computer simulation of a camera lens with a 24 mm focal length and f-stops (lens apertures) that roughly correspond to the maximum and minimum pupil sizes demonstrates depth of field, i.e., the minimum and maximum distances that are completely in focus, for a subject about half a meter from the lens.

[2] Photographers use blur creatively when they employ a wide aperture to capture their subject in a shallow depth of field and throw the background out of focus. The effect, called bokeh, is used frequently in portraits and elsewhere for aesthetic effect or to eliminate cluttered backgrounds. Apple popularized the term in 2016 when it introduced "portrait mode" in iPhone cameras, which digitally simulate the bokeh effect produced by the lens of a single-lens reflex camera. The contrary effect "deep focus" is also important in visual storytelling. Seamless transitions between selective focus and deep focus via image integration is largely unconscious for most people, most of the time. The value of "generalists in love with details" (a phrase attributed to Stewart Brand) suggests a metaphor of transitions from the narrowly defined "visual" into the more inclusive and imaginative "visionary".



8 mm pupil size (aperture ~ f2.1)   1.7 mm pupil size (aperture ~f8.3)

Pupil dilation in near darkness   Pupil constriction in bright light

Figure 153 : Simulated depth of field for a subject 0.5-0.8 meters from the lens. Source: DOF Simulator. https://dofsimulator.net/en/

Compare the depth of field with image blur as a function of apparent distance in Leonardo's *Salvator Mundi* (fig. 154). Note the sharpness of focus on fingers and smocking and the blur of the slightly more distant face.

Figure 154 : Leonardo's Salvator Mundi (c. 1504-1510). Source: Wikimedia Commons.

Leonardo's notebooks give instruction concerning the optimum light for portraits. These are conditions under which the artist's pupils are expected to be large because of the dim light.

Consequentially, the optical depth of field will be small. Another effect due to the interface of rod and cone cells in the eye will be discussed later with reference to the *Mona Lisa*.

The fovea of the retina

Visual resolution is greatest in the small area of the retina called the fovea [10]. The retina is approximately 30-40 mm in diameter. The fovea is only about 1.5 mm in diameter and thus covers only about 5 percent or less of the light-sensitive surface. At any one instant, only a small part of the visual field is perceived with the highest resolution. By moving our eyes, we normally construct a more detailed mental image of the world than ever existed on the surface of the retina or its immediate transformation into neural impulses at any one moment (fig. 155).

Martin Kemp notes that Leonardo's selective use of focus is not limited to a simple plane as occurs in depth of field or the minimum distance required from a fixed lens. Leonardo sometimes marks distinct degrees of focus for different features at the same distance, as in the *Salvator Mundi*:

He knew that at very close ranges, of a few inches or less, that sharp perception was impossible — though he did not know that this was caused by the focal length of the lens. Christ's hands are at the optimum distance — far enough away and yet close enough to be seen as sharply as the eye could manage. However, the 'soft focus' effect of more distant forms is not observed with complete consistency, since, unsurprisingly, the vivacious vortices of the hair are more crisply painted with little curves of delicate impasto, while the adjacent features of the face are painted more softly. Leonardo's so-called *sfumato* is, as we shall see, selectively and instinctively tuned to act in concert with the desired pictorial effects [11].

By hypothesis, the different foveal areas of sharp focus are rendered in temporal instants that most of us combine into sharper mental images of the entire visual field. In this way, we use an "illusion" akin to flicker fusion frequency (See companion paper [12]: "Evidence for extraordinary visual acuity in Leonardo's comment on a dragonfly") to form a mental image of the world that is more globally in focus and of higher resolution than was ever present on the retina at any single instant. Three hypotheses come to mind regarding Leonardo's possible involvement with this mechanism regarding the variable level of focus evident at an equal distance:

1. By virtue of possessing a fast flicker fusion frequency, Leonardo may have noticed and visually remembered quick flashes of vision, such as hair in sharp focus but face in soft focus.
2. Leonardo may have been able to hold a steady gaze suppressing normal eye movement for long periods, and therefore possessed selective focus without the need for additional temporal resolution.
3. Leonardo may have come upon the evocative power of selective focus without his own direct experience of it.

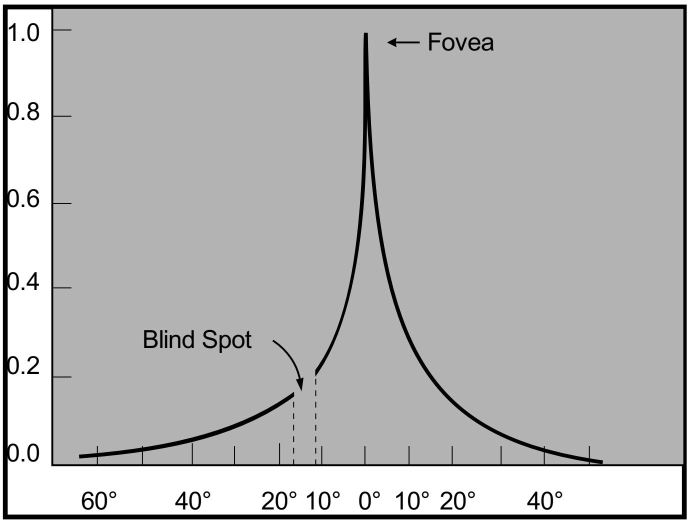


Figure 155: Relative acuity of the human eye as a function of degrees from the fovea

Source: Wikipedia, Fovia Centralis, https://en.wikipedia.org/wiki/Fovea_centralis

Physical optics

The history of optics will not be reviewed here other than to say that the systematic formulation for the pupil/aperture effect on sharpness of focus occurred in the mid-19th century with major contributions by Ernst Abbe [13].

A psychophysical contribution to the subjective apprehension of depth of field

The three-dimensional visual world that most of us live with most of the time is the construct of our brain assembling multiple images at many different planes of focus [14]. By hypothesis, this stitching of focal planes is related to the viewer's flicker fusion frequency (FFF). It seems ironic that the same mental function that leads to a blur of motion allows for a more accurate subjective rendering of stationary space. A companion manuscript presents the hypothesis that Leonardo had a critical flicker fusion frequency (CFFF) at either the high end or beyond the normal range [12]. The awareness, skill, and possibly genetically enabled ability to "freeze frame" movement is, by hypothesis, similar to that for either holding or remembering the narrow focal planes of focus from which most of our experience of the three-dimensional external world is seamlessly and unconsciously constructed.

Learning how to use a conventional light microscope is perhaps analogous to learning how to see with the naked eye, although the latter process probably occurs unconsciously and at a younger age. A beginner at microscopy consciously learns to mentally construct three-dimensional images of specimens that are not all in focus at any one moment. This is necessary because the depth of focus of the optics is often less than the physical depth (Z-axis) of the specimen. As this skill is mastered, it retreats from conscious awareness. The experienced microscopist usually has one hand on the focus knob and continuously moves the focal plan up and down through the specimen without thinking about it (see figure 156). The other hand may be on the knobs controlling horizontal (X-Y) stage movement from side to side and forward and back, which facilitates horizontal stitching. The mind of an experienced microscopist has learned to build up a three-dimensional image of the specimen. Optics and psychophysics are consistent with the idea that normal vision works in similar ways. By hypothesis, Leonardo noticed that instantaneous vision is only partly in focus, and this insight, whether conscious or not, formed a basis for his sfumato in portraits.

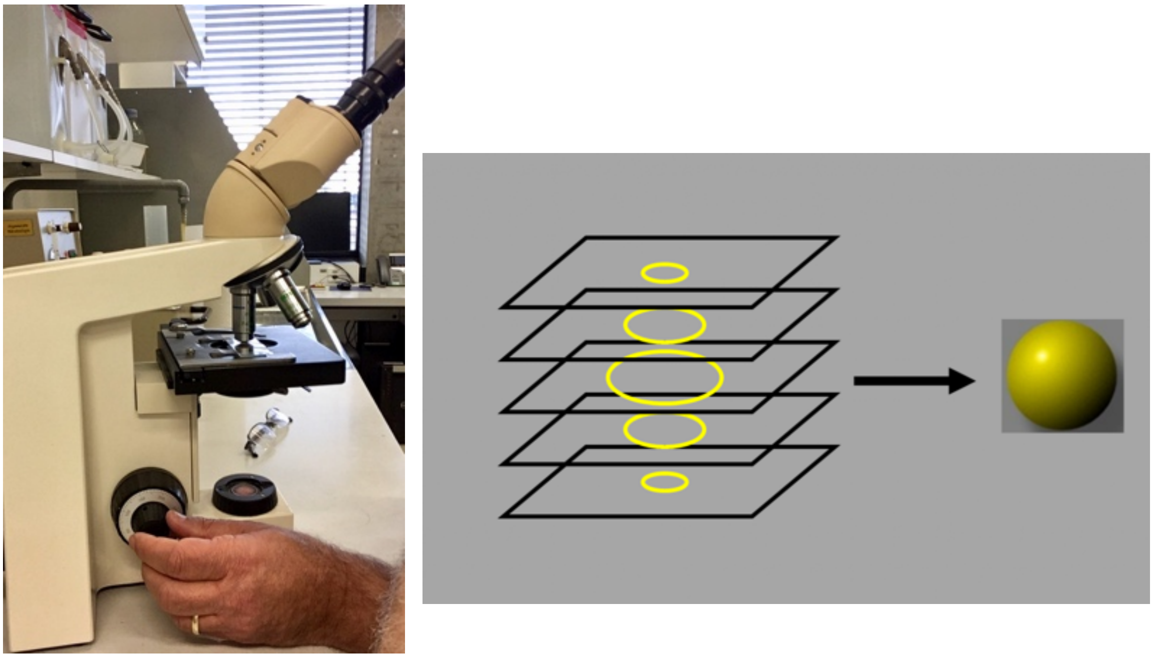


Figure 156 : Microscopists continuously adjust the focus knob (left) to move the visual plane of focus up and down through the specimen. By integrating separate planar views of the specimen (right), a microscopist's mind constructs a three-dimensional view.

Source of diagram: Northwestern University Center for Advanced Microscopy. https://cam.facilities.northwestern.edu/588-2/z-stack/

It is a common subjective experience that when paying undivided attention to a nearby object or person, the background, if it is noticed at all, is out of focus. By hypothesis this is because the one-pointed attention has prevented the back-and-forth focus that is usually integral to forming a holistic in-focus image of our surroundings. Leonardo's use of sfumato is discussed most often in the context of perspective at distance and the perception of looking through a hazy atmosphere. I am not aware of its being discussed as the subjective experience of focused attention in which the usual mental integration of many focal planes is disrupted by continuous concentration on one focal plane. Again, note the Z-axis of the focal plane in the *Salvator Mundi*.

Attention, affection, and concentration also drive pupil size

A significant literature that will not be reviewed here discusses change in pupil size as an indicator of emotional and intellectual states of mind. Pupils dilate in contexts of affectionate attention and intellectual concentration. In general, the effects of light are quantitatively greater, but in constant light other effects become easily measurable and are among the most reliable physiological indicators of psychological states [15].

The Renaissance concept of beautiful eyes may have featured large pupils

Secondary sources claim that the Renaissance concept of beautiful eyes had large pupils. This is consistent with the large but not dilated pupils seen in several portraits, including *Portrait of a Musician* (c. 1483-1486), whose asymmetric pupils have been discussed previously [16, 17], and the *Mona Lisa* (c. 1503-1515). Primary sources on this point would be welcomed.

A possible pharmacological connection

Belladonna means "beautiful woman" in Italian. The plant *Atropa belladonna* produces the drug atropine. Atropine dilates the pupil; it is used routinely for this purpose in eye examinations. It has been suggested that in Renaissance Florence the pupil-dilation effect of *Atropa belladonna* was deliberately used as a cosmetic [18, 19].

Pupil size allows inference of the light level at which a portrait was painted

Ambient light level is a strong driver of pupil size. Assuming the artist was in the same light as the subject, the artist's pupil size was similar to that of the subject. The artist's depth of field can thereby be inferred. Leonardo's calculated depth of field can then be compared with the sfumato and blur in a portrait. Two caveats apply: (1) There are several formulas for calculating the relationship between pupil size and depth of field, and although they mostly coincide at maximum and minimum, the different models differ significantly at intermediate light levels [20], and (2) There is significant variation in light sensitivity among individuals. Causes of this variation are not fully known. With these caveats, pupil size of the subject in a portrait by Leonardo allows one to see how closely he followed his own advice concerning the ambient light level at which portraits should be painted:

Of the selective light which gives most grace to faces

When you want to take a portrait do it in dull weather, or as evening falls, making the sitter stand with his back to one of the walls of the court yard. Note in the streets, as evening falls, the faces of the men and women, and when the weather is dull, what softness and delicacy you may perceive in them….paint a work towards evening or when it is cloudy or misty, and this is a perfect light.

https://en.wikisource.org/wiki/The_Notebooks_of_Leonardo_Da_Vinci /IX

Consider the *Mona Lisa* of the Louvre

A reasonable estimate is that her pupils are between 4 mm and 5 mm in diameter. The inferred light level is between 1 and 10 candles per square meter (cd/m^2), which is the center of the mesopic vision range, the light range where both rods and cones in the retina are jointly engaged (Fig. 157). Only under the mesopic light conditions favored by Leonardo for portraits are both rods and cones active at the same time. At these intermediate levels of illumination, there is a unique combination of simultaneous rod-dependent apprehension of contrast and also cone-dependent resolution of color and temporal differences. Rods are more numerous than cones. So, when both are engaged, spatial resolution is also highest because an important limit to spatial resolution is a difference in illumination of nearby light-sensitive retinal cells. Unique aspects to both image acquisition and neuronal processing emerge only during dusk or dull-day conditions, where both rods and cones are active and synergizing.

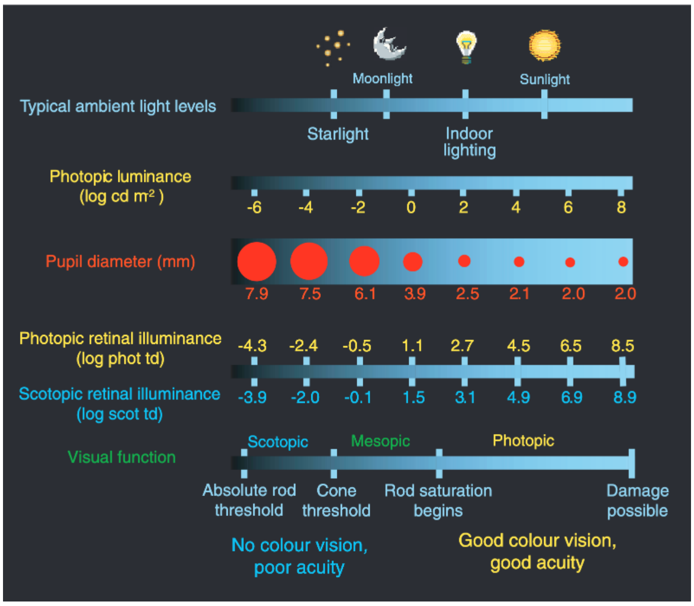


Figure 157: Visual effects of different levels of external illumination. Photopic luminance, measured in candles per square meter, expresses light levels of particular spectra of light, i.e., what fraction of the intensity occurs at each wavelength in the visible spectrum. Retinal illuminance, measured in Trolands (td), refers to the level of illuminance entering the eye through the pupil and impinging on the retina. Photopic (bright light) retinal illuminance and scotopic (dim light) retinal illuminance differ in the light spectra for which typical cone and rod cells are most sensitive. Visual function refers to which visual cells are active under given light conditions. Rod cells dominate under scotopic light conditions; they are more sensitive to low light and better at sensing contrast. However, rod cells to not distinguish different colors and they are not good at detecting rapid changes in light levels (that is, rod cells have a slower flicker fusion frequency). Cone cells dominate vision under bright light (photopic) conditions. They are able to distinguish different colors and they have a higher flicker fusion frequency but are inferior to rods at sensing contrasts.

Source: From Figure 1 of reference 21.

The soft focus and shallow depth of field Leonardo saw in “dull weather or as evening falls” may be seen in the left panel of figure 152 showing of a chessboard imaged by the electro-mechanical eye with a 5 mm pupil size and, by hypothesis, also in the *Mona Lisa*.

Four mechanisms — pupil dilation, temporal integration, foveal acuity, and mesopic rod-cone synergy — all contribute to sfumato-relevant aspects of what one sees under the conditions Leonardo recommends for portrait painting. Leonardo did not articulate any of these in the same verbal and diagrammatic manner that he did with perspective and anatomy. Indeed, the conceptual, experimental, and verbal articulation of these mechanisms did not occur until four centuries later in the case of pupil size, or five centuries later in the case of flicker-fusion-like integration of multiple images, foveal hyper-acuity within the retina, or the intermediate-dim light levels at which rods and cones function synergistically. Leonardo very likely sensed these effects, perhaps unconsciously in the realm of his artistic sensibility, even though he did not and perhaps was not consciously able to name them. All four mechanisms — and perhaps others as yet undiscovered — underlie Leonardo’s statement that the dim light of dusk or overcast days most favors the appreciation of faces:

Note in the streets, as evening falls, the faces of the men and women, and when the weather is dull, what softness and delicacy you may perceive in them.

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References

KEMP M. (1977) : Leonardo and the visual pyramid. *Journal of the Warburg and Courtauld Institutes*, 40:128-149.

KEMP M. (2006) : Leonardo da Vinci : The Marvelous Works of Nature and Man, 2nd edn: *Oxford University Press*.

ISAACSON W. (2017) : Leonardo da Vinci : The Biography. *London: Simon & Schuster*.

KEMP M. (1971) : 'Il concetto dell'anima' *In* Leonardo's early skull studies. *Journal of the Warburg and Courtauld Institutes*, 34:115-134.

LUMLEY H. de, LUMLEY M.-A. de, CLARAC F., FIGARELLA J., LAMY P. : (2017) : Leonardo da Vinci . Pioneer of comparative anatomy, biomechanics and physiognomy. *International Journal of Anthropology*, 32:3-76.

RADMAN Z. (ed.) (2013) : The Hand, an Organ of the Mind: *The MIT Press.*

APTHORP D., SCHWARZKOPF D.S., KAUL C., BAHRAMI B., ALAIS D., REES G. (2013) : Direct evidence for encoding of motion streaks in human visual cortex. *Proc Biol Sci*, 280(1752):20122339.

KEMP M. (1992) : In the beholder's eye: Leonardo and the "Errors of Sight" in theory and practice (Hammer Prize Lecture). *Achademia Leonardi Vinci,* V:153-162.

PETSCH S., SCHUHLADEN S., DREESEN L., ZAPPE H. (2016) : The engineered eyeball, a tunable imaging system using soft-matter micro-optics. *Light-Sci Appl*, 5.

BRINGMANN A., SYRBE S., GORNER K., KACZA J., FRANCKE M., WIEDEMANN P., REICHENBACH A. (2018) : The primate fovea: Structure, function and development. *Prog Retin Eye Res*, 66:49-84.

KEMP M., SIMON R., DALIVALLE M. (2019) : Leonardo's Salvator Mundi and the Collecting of Leonardo in the Stuart Courts: *Oxford University Press.*

THALER D.S. (2019) : Evidence for extraordinary visual acuity in Leonardo's comment on a dragonfly *Manuscript available on request from davidthaler@unibasch; davidsthaler@gmailcom.*

ABBE E. (1881) : VI1.-On the estimation of aperture in the microscope. *Transactions of the Royal Society*:388-423.

MARCOS S., Moreno E., Navarro R. *(*1999) : The depth-of-field of the human eye from objective and subjective measurements. *Vision Res*, 39(12):2039-2049.

KAHNEMAN D., Beatty J. *(*1966) : Pupil diameter and load on memory. *Science*, 154(3756):1583-1585.

SHAIKH S. (2007) : Eyes on Ice & No Blind Mice: Visions of Science from the Science of Vision: *AuthorHouse*.

TYLER C.W. *(*2019) : Evidence that Leonardo da Vinci had strabismus. *JAMA Ophthalmol*, 137(1):82-86.

STEVENS S.D., K' LARNER A. (1990) : Deadly Doses: A Writer's Guide to Poisons: *Writer's Digest Books*.

HOLZMAN R.S. *(*1998) : The legacy of Atropos, the fate who cut the thread of life. *Anesthesiology*, 89(1):241-249.

WATSON A.B., YELLOTT J.I. *(*2012) : A unified formula for light-adapted pupil size. *J Vis*, 12(10):12.

QUESTIONS À DAVID THALER ET RÉPONSES

Jeffrey Laitman : Merci David, c'était brillant, j'ai trouvé cette présentation excellente j'ai une question pour vous. Récemment les individus ont découvert beaucoup de choses sur le contenu de ce que nous appelons les fluides endolymphe et périlymphe dans l'oreille interne, essentiellement du potassium. L'oreille interne, en particulier le système vestibulaire et le système de l'équilibre, sont de plus en plus reliés au mouvement des yeux, d'une façon encore mal comprise. Est-ce que vous ou vos collègues avaient déjà lu ou réfléchi à la façon dont des changements dans les gènes que vous avez mentionnés pourraient avoir un lien avec la position de la tête, ce qui, par des actions subtiles, pourrait être liée également à l'activité de l'œil?

Jeffrey Laitman : *That was brilliant, I thought that was great. I have a question for you. Recently, individuals are discovering more and more about the contents of what's called endolymph and perilymph fluids in the inner ear, which are heavily based on potassium as an important element of these. Inner ear, particularly the vestibular system and balance system, is more and more being shown to be related to eye movements, and a coordination that is not fully understood. Have you read or any of your colleagues given thought to how changes in the content in the genes that you have mentioned may relate to positional relationships of head, which of course, in subtle actions, could relate to eye activities.*

David Thaler : Le canal potassique KV 2.1 est largement exprimé. KV 8.2 ne l'est pas, il est restreint aux cônes. Le canal est un tétramère, parfois il y a formation d'un hétéromère. Personnellement, je ne connais pas l'oreille interne, mais j'ai quelques connaissances sur les canaux potassiques et dans la littérature, nous pouvons discuter de nos ignorances respectives et où va la connaissance car il y a beaucoup à dire… Et bien entendu, la teneur en sel dans le milieu pourrait également avoir un impact important, donc si vous en avez trop dans les fluides extracellulaires, j'imagine qu'il y aura un effet physiologique important.

David Thaler *: The KV 2.1 potassium channel is very widely expressed. The KV 8.2 is not, it's pretty restricted to the cones. The potassium channel is a tetramer, and you can have a heteromeric formation. I personally know nothing of the inner ear, but I'm accumulating some knowledge of the potassium channels although, believe me, it's a deep literature, decades of it, and we can discuss a little bit to share our ignorance and where it might go. I'd be happy to… and of course, there are osmotic issues, so the general level of salt in the solution, regardless of the particular channel, could have a profound effect. So if you build up too much in the extracellular fluid, I could really imagine that having a strong physiological effect.*

Jeffrey Laitman : On n'en sait pas beaucoup sur ce sujet, on commence seulement à voir que cela a une influence sur les mouvements de la tête mais cela fait 20 ans seulement que nous apprenons là-dessus et sur le traitement du glaucome. Il y a encore beaucoup de points d'interrogation pour tout ce qui est de l'oreille interne.

***Jeffrey Laitman**: But we know relatively little about vestibular system movements. It's just being shown more and more important in visualization and subtle head movements, and one of the key components are going to be the content of the fluids. It's only been over the last 20 years that we learned about ocular fluids. That's how come glaucoma can be treated. Still, diseases of the inner ear world are still a huge question mark...*

David Thaler : Est-ce qu'il serait possible de mesurer l'osmoralité du potassium de ces fluides cellulaires libres ? Je pense que ce serait la suite la plus simple à donner.

***David Thaler**: So the question I'm asking is, is it possible to measure the potassium osmolarity of the cellular free fluids? That would be the simplest way to go.*

Jason Organ : Merci beaucoup, c'était excellent. Ma question concerne les différences. Je pense que vous avez dit que votre 2e gène était exprimé d'avantage que l'autre c'est bien ça?

***Jason Organ** : That was really excellent, thank you for that. I have a question about differences in expression… wait, I think you said that your second candidate gene was expressed more in cones than anything else... is that correct, or more than the other one?*

David Thaler : Le gène 2.1 est exprimé dans de nombreux cas alors que le 8.2 dans des cas plus limités, dans les cônes il s'agit d'un hétéro-tetramère.

***David Thaler:** Well, the 2.1 gene is very expressed throughout the body in many cases, the KV 8.2 is more restricted, and in the cones it's a hetero-tetramer.*

Jason Organ: Certains primates ont une vision trichromatique, d'autres ne l'ont pas, et il y a une très grande variation des types de cônes dans le monde animal, selon les espèces. J'aimerais savoir ce que vous en pensez et en quoi cela pourrait avoir un impact sur votre interprétation de l'acuité visuelle des libellules comparée à celle des êtres humains et si les rétines sont assez similaires pour faire ce genre de prédiction.

***Jason Organ**: Ok so, with regard to that, you know some primates have trichromatic vision, some don't, and there's a huge variation in the types of cones that are available for the animal world and what has evolved in different taxa... I'm curious to know how you might or what you have to think about the head, and how that might affect the way you're interpreting dragonfly visual acuity versus human visual acuity, and whether or not the retinas are even remotely similar enough to make these kinds of predictions.*

David Thaler : Il y a des différences importantes certainement entre les mammifères et les insectes, ne serait-ce que dans le nerf optique, si les cellules des cônes hyperpolarisent ou dépolarisent en fonction de l'excitation optique. Ce sont des questions hautement techniques. Vous faites vous-mêmes des comparaisons anatomiques depuis des années et ces comparaisons très approfondies sur le plan électrophysiologique sont bien plus avancées que le quelques semaines que j'y ai moi-même consacrées.

***David Thaler**: There are significant differences certainly between mammals and insects. Even the bias of the optic nerves coming out, and whether or not the cone cells hyperpolarize or depolarize as a function of being excited, optically. So these are deep technical questions, we really have to go to the mats about it. I mean, you guys do deep comparative anatomy over years, and this kind of deep comparative electrophysiology is something that people have dedicated a lot more than the last couple of weeks to it, which is all I have done.*

Jason Organ: Je me demande comment la vision chez les primates peut être différente, je pense que les libellules n'ont pas de vision stéréoscopique contrairement aux singes, leur vision est juste différente.

***Jason Organ:** Similarly, I wonder how stereoscopic vision in primates actually might affect this. It's different… my understanding of dragonflies, they don't have stereoscopic vision they have just very different vision than we do.*

David Thaler *:* En fait, il est possible de mettre des lentilles de contact bourrées d'électrodes qui permettent de faire des mesures intéressantes et les enregistrements intracellulaires qui nous ont permis d'identifier les réseaux de potassium dont j'ai parlé tout à l'heure nous permettent d'avancer. Chez les primates, il faut se poser la question de savoir quel degré d'information vous souhaitez avoir véritablement, jusqu'où vous voulez mener des expériences.

***David Thaler :** Well, the extracellular electrodes, the contact lenses with electrodes could presumably be applied to many systems, and the intracellular recording that identify the potassium channels, you're not in a position to do that to too many people, and for primate experiments one has to really ask oneself how much you want to know, how much do you really want to know, experiment.*

Marguerite Mangin *:* Je me souviens avoir entendu à maintes reprises que Léonard avait une vision tétrachromatique, est-ce que vous pensez que cette hypothèse est bonne ?

***Marguerite Mangin** : I seem to remember or have heard many times that Leonardo was supposed to have a tetrachromatic vision. Few humans have this possibility. Have you thought about that versus the regular trichromatic that we all see, I think ?*

David Thaler : Je n'ai recueilli aucune preuve au cours de mes études de ce fait. Encore une fois, je sais que Tom Dagmar par exemple a émis l'hypothèse selon laquelle certaines personnes, 2 à 3 pour 100 de l'humanité possède un gène opsine en plus. J'ai lu beaucoup de choses différentes. Il y a des personnes qui apparemment arriveraient à distinguer les couleurs différemment, mais Léonard n'a rien fait qui soit invisible à notre œil. On peut voir toutes les nuances de ses travaux et pour ce qui est de l'élément spatial, Cesare Marchetti dans une publication parlait de 100 microns de distance entre les lignes. Il faudrait travailler sur la temporalité et c'est ce qui nous permettrait de savoir s'il y a des qualités surhumaines chez certaines personnes.

***David Thaler** : Well, I wasn't able to see any evidence in my own. I mean it's again this issue of whether you have enhanced… - I know that Tom Dagmar, for instance, speculated that maybe you have an extra cone, that maybe like one or 2% of people have an extra opsin gene, and there's some literature - I looked at the papers, quite controversial - that people might be able to distinguish colors a little more. Clearly, Leonardo didn't make anything that is invisible to us, right? I mean, people have looked by this time with many enhanced spectral means. And similarly, with the spatial things, although it's clear that he was very articulate, the closest lines – it was Cesare Marchetti who mentioned it in a publication - are about 100 microns apart, those are normal range of human, so it's only with the timing that I could get any evidence of - if you want to call it – superhuman, or beyond normal motion apprehension.*

Michael Kwakkelstein : Lorsqu'on voit tomber une goutte d'eau, on sait comment ça se passe parce that you mention this extra capacity, the deformation of the drop. qu'on a vu les ralentis mais lui n'avait pas accès à ce type de technique alors comment a-t-il fait ?

***Michael Kwakkelstein :** It's just about that he also saw the drop of water… When a drop of water falls, and then how it goes up, I know that we only know of that in slow motion, so I was wondering how could he have seen that, now*

David Thaler : On ne peut pas connaître les expériences qu'il a faites mais pour revenir à la libellule c'est par l'observation qu'il a réussi à arriver à ses conclusions.

***David Thaler:** That's an excellent point, and I think that we should discuss how clearly one can interpret what experiment he did, and then actually try to put a timing number on it, because the dragonfly wing is so far at the edge of one's fingernail's ability to put a number and there might be another one.*

Amalie Rothschild *:* Tout d'abord, c'est fascinant bien entendu, je pense que Léonard avait une acuité visuelle extraordinaire et qu'on retrouve aussi certaines choses chez les personnes atteintes d'Asperger. Einstein et d'autres esprits parmi les plus brillants avaient très clairement des capacités de concentration extraordinaires. La vision est une chose qui peut expliquer une partie de son génie mais elle n'est qu'une partie de son génie parce que d'autres personnes pouvaient avoir aussi des visions extraordinaires sans toutefois avoir la curiosité et la capacité de concentration que Léonard avait et qui faisait de lui l'homme qu'il était. Je ne vois pas la différence entre la vision de la libellule et l'utilisation par Léonard de la libellule dans ses dessins. On parle ici de sa capacité à voir le mouvement des ailes de la libellule et d'avoir utilisé cela dans son analyse de la vie.

Amalie Rothschild: *First of all this is fascinating of course, and I would take as a given that Leonardo certainly had extraordinary powers visually, perhaps more than some of us normally do. I think what was also raised before about the possibility of being on the autism spectrum, Asperger's, explains a great deal. We know that Isaac Newton, Einstein, many of the most brilliant minds of scientific and other areas clearly had very extraordinary abilities of concentration. The vision is one thing, it might explain a part of his genius, but it's only a part because there are other people who might have extraordinary vision, but they don't have the curiosity, the concentration, all of the other characteristics that are involved with making this person be what he was, and do what he did. So I'm curious… I also didn't understand, I don't see the difference between the vision of the dragonfly and Leonardo's use of the dragonfly for his drawings… what we're talking about his ability to have seen the motion of the wings, and to use it as part of his analysis of flight etc.*

David Thaler : Cette vidéo illustrait parfaitement la fréquence de diffusion de clignotement et pour illustrer le mouvement rapide. Mais le fait que la libellule bouge rapidement, elle peut voir rapidement, tout cela va de pair, les insectes qui sont plus lents ne voient pas aussi rapidement non plus, surtout la nuit, bien sûr.

David Thaler*: That dragonfly was a beautiful video to teach flicker fusion frequency, and to illustrate that it happens to have a fast one. I didn't mean to say... but the fact that it can move fast and see fast do go together, and the flies who move much more slowly and at night have much slower time apprehension, of course.*

Amalie Rothschild *:* Est-ce qu'on a des preuves que Léonard avait fait ses propres expériences par exemple, il aurait pu étudier les insectes, il aurait pu les mettre dans un pot en verre pour essayer de ralentir les mouvements. Est-ce qu'on sait si ça s'est produit?

Amalie Rothschild : *Is there any evidence that Leonardo did any experiments of his own, like he could have had some insects caged, in drawers, or drugged in order to slow their motion down in order to do some of his drawings ? Is there any indication of those kinds of aspects of how to study them?*

David Thaler : Phil Richardson qui a étudié le code sur le vol des oiseaux de Léonard, pense qu'il a pu observer une libellule à un moment, au crépuscule, quand le soleil formait le bon angle, elle rasait le sol plus foncé. Il l'aurait vue très brièvement et ne l'a plus jamais observée par la suite.

David Thaler: *Phil Richardson who studied Leonardo's codex on the flight of birds, emailed me that he thinks he saw it once over dark grass when the sun was at the right angle, but then the dragonfly angled across 2 lanes of traffic and he couldn't follow it and he's never been able to see it again since...*