

FROM NEURAL MECHANISMS OF SHORT-TERM MEMORY TO THE COMPUTATIONAL ARCHITECTURE OF THE HUMAN BRAIN

Anonymous authors

Paper under double-blind review

ABSTRACT

Since 1840, it has been known that the cerebral cortex of the human brain mainly consists of six layers. What is the computational architecture of this multi-layer computing machinery? This problem is certainly worth investigating and is interesting to many researchers in cognitive science & neuroscience on the one hand and computer science & engineering on the other. The present paper tackles this problem from a new perspective—namely, starting from the visual phenomenon of seeing blind spots as afterimages, to determining the neural locus of afterimages, to conceptualizing afterimages as visual short-term memory, and finally to formulating a computational architecture of the brain. First, presently, all the textbooks in vision science and perceptual psychology do introduce afterimages but also ubiquitously assume them as due to some peripheral adaptation mechanisms occurring in the retina of the eye; here, the long-forgotten phenomenon of seeing blind spots as afterimages is revived and is used as an *instantia crucis* to demonstrate the cortical origin of afterimages. Second, correlating this phenomenon with the neuroanatomical fact that the blind spot is represented within V1-L4 (i.e., Layer 4 in the visual cortical area V1), it is deduced that V1-L4 is the neural site for afterimages. Third, it is further deduced that the overall computational architecture of the brain is as follows: In each visual cortical area, the superficial layers (i.e., L2&3) constitute a feedforward neural network for transforming information from one level to the next, the deep layers (i.e., L5&6) constitute a feedback one for the reverse transform, and the middle layer (i.e., L4) serves as short-term memory. Finally, it is discussed how the computational architecture of the human brain conceptualized in this manner may help foster interdisciplinary interactions towards a more complete understanding of the human brain.

1 INTRODUCTION

Under certain visual conditions, when a viewer sees a stimulus, they may continue to see an image of the stimulus even after the physical stimulus has already disappeared: This visual phenomenon is known as an afterimage. A basic and prominent issue pertinent to afterimages is where they occur in the human visual system: Are they merely some adaptation mechanisms happening in the retina of the eye (hereafter, this view will be referred to as the Retinal View)? or are they a form of visual memory residing in the brain (hereafter, the Brain View)? Table 1 lists some major publications concerning afterimages since the time when Newton (1691) communicated his observation of afterimages: As we can see, there have been proponents of both of these two views. In the present paper, we will demonstrate that the Retinal View is erroneous and only the Brain View is correct.

The topic of afterimages is universally taught in all the textbooks in vision science (e.g., Palmer, 1999, pp. 105 & 109) and in perceptual psychology (such a course may be known as “Sensation and Perception”; e.g., Wolfe et al. (2021), pp. 153-155). About a decade ago, essentially all such textbooks had subscribed only to the Retinal View. Presently, the situation is changing—for example, Zaidi et al. (2012), Wolfe et al. (2021) advocate a hybrid view as follows: “Adaptation occurs at multiple sites in the nervous system, though the primary generators are in the retina” (p. 155): The

Table 1: Major publications on the Retinal View vs. the Brain View with regard to afterimages

Investigator(s)	Phenomena / Arguments	The Retinal View	The Brain View
Newton (1691)	He observed interocular transfer of afterimages and briefly suggested: “It [afterimage] seems rather to consist in a disposition of the sensorium [the part of the brain for sensation] to move the imagination strongly” (p. 154).		✓
Darwin & Darwin (1786)	Adaptation: analogy between the retina and the muscular system	✓	
Binet (1886)	Interocular transfer (pp. 43-45)		✓
Delabarre (1889)	Interocular differences of seeing the same afterimage	✓	
Craik (1940)	Retinal anoxia (“blinding” an eye by finger-pressing it) disrupts afterimage.	✓	
Weiskrantz (1950)	Afterimage may be produced from imagination.		✓
Urist (1958)	Pushing an eye’s ball, the eye’s scene view shifts in position but its afterimage stays.		✓
Loomis (1972)	Afterimages from long-duration light stimulation with little bleaching are correlated with visual appearance.		✓
Levay et al. (1985)	Discovery of a cortical representation of the physiological blind spot in V1-L4 in the macaque monkey’s brain.		
Shimojo et al. (2001)	Filling-in visual surface may generate afterimage.		✓
Tsuchiya & Koch (2005)	Interocular influence on afterimage formation		✓
Adams et al. (2007)	Discovery of a cortical representation of the physiological blind spot in V1-L4 in the human brain.		
Shevell et al. (2008)	Interocular misbinding of color and form		✓
Zaidi et al. (2012)	Physiological recordings in the macaque monkey’s brain	✓	✓
Dong et al. (2017)	The Breese effect (Breese, 1899) : binocular rivalry between two eyes’ afterimages slower than that with physical stimuli.	✓	✓
Kronemer et al. (2024)	Shared mechanisms between afterimages and visual imagery		✓
Kittikiatkumjorn et al. (2025)	Afterimage color is factored by color constancy.		✓

108 Retinal View is still a component in this hybrid view; hopefully, the Retinal View would become
 109 totally abandoned in another decade or so.

110
 111 As shown in Table 1, the Brain View regarding afterimages’ localization in the human visual system
 112 is not new at all: Newton (1691) was already suggesting it. However, only in the last several decades,
 113 there have been accumulating many lines of evidence in support of the Brain View. In this respect,
 114 two particularly relevant and critical findings are as follows: (1) Levay et al. (1985) delineated a
 115 representation of the physiological blind spot in Layer 4 of the primary visual cortex (also known as
 116 the cortical area V1; hereafter, Layer 4 of V1 will be referred to as V1-L4) in the macaque monkey’s
 117 brain, and Adams et al. (2007) found the same in the human brain; (2) We recently rediscovered
 118 the phenomenon of a human observer being able to see their own physiological blind spot as an
 119 afterimage and correlated this phenomenon to the neuroanatomical finding by Levay et al. (1985)
 120 and AAdams et al. (2007). Together, these recent advances decisively and precisely pinpoint the
 121 first-stage neural substrate of afterimages to V1-L4.

122 In this paper, we will build upon the above-mentioned recent advances and establish a neural theory
 123 of afterimages consisting of the following tenets: 1. Positive and negative afterimages share the same
 124 neural substrate: The first-stage is V1-L4, and the subsequent stages are the layer 4s in other visual
 125 cortical areas—in this respect, we will substantiate the Brain View about afterimages into a concrete
 126 form; 2. Afterimages constitute a form of short-term memory (STM) in the brain; 3. In terms
 127 of the neural computational architecture of the brain, for each cortical area, STM is sandwiched
 128 between a feedforward neural network and a feedback counterpart—it may play a computational
 129 role for variable binding. Finally, we discuss potentially fruitful bidirectional interactions between
 130 perceptual & neuroscientific researches in biological vision on the one hand and computer science
 131 & engineering endeavors in artificial / machine vision on the other.

132 2 PHYSIOLOGICAL BLIND SPOTS, AFTERIMAGES, AND NEURAL 133 LOCALIZATION

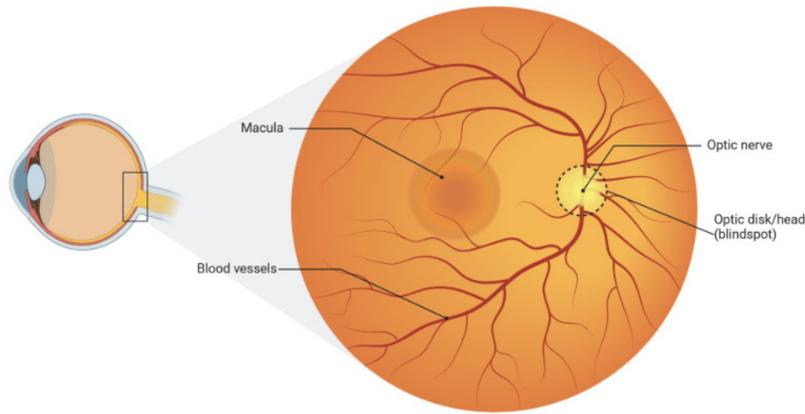
134 2.1 THE PHYSIOLOGICAL BLIND SPOT IN THE EYE

135 We have a physiological blind spot in each of our eyes: It corresponds to a port of the eye’s retina
 136 (anatomically known as the “optic disk”) where no photoreceptors (i.e., rods and cones) exist, where
 137 optic nerve fibers exit the eye, and where blood vessels enter and exit the eye (i.e., arteries entering
 138 and veins exiting the eye). This anatomical feature of the eye is clearly seen in Figure 1(a) which
 139 shows an image of a human eye’s retina as seen by an ophthalmologist (i.e., eye doctor) when
 140 examining someone else’s eye with some retina imaging device. The shortened term “blind spot”
 141 may mean various things in different contexts; hereafter, we will use it to refer specifically to the
 142 physiological blind spot in the eye.

143 The blind spot was discovered by the French scholar Edme Mariotte around 1668: It is certainly
 144 an amazing scientific discovery. Mariotte’s method demonstrating the blind spot, however, is about
 145 how to locate it within the viewer’s visual field, not about how to (consciously) see it. Presently,
 146 all the textbooks in perceptual psychology, vision science, neuroscience, and ophthalmology, when
 147 mentioning about the blind spot, describe this method only (e.g., Wolfe et al., 2021, p. 40). This
 148 method / procedure of demonstrating the blind spot is illustrated in in Figure 1(b).

149 Under special conditions, it is actually possible for the subject (i.e., the owner of the eye; we may
 150 also refer to him/her as the viewer or observer) to see their own blind spot in each eye, literally see-
 151 ing the blind spot as a black hole on a lighter background or a white hole on a darker background,
 152 as illustrated in Figure 1(c) and (d) respectively—more generally, a colored spot on a background of
 153 the spot’s complementary color; the BS may, or may not, be accompanied by the Purkinje Tree (PT)
 154 which denotes the image of retinal blood vessels. As far as we have been able to trace back, this
 155 phenomenon was first reported by the French scholar Philippe de La Hire (1640-1718) in La Hire
 156 (1694): Henceforth, we will refer to this phenomenon as the La Hire phenomenon. It was subse-
 157 quently rediscovered and extended by the Czech scientist Johann Evangelist Purkinje (1787–1869)
 158 in Purkinje (1819): Figure 1(c) is an entoptic vision based on Purkinje’s original drawing of his
 159 observation of his right eye’s blind spot and retinal blood vessels as well as the present authors’ own
 160 observations. More broadly, Purkinje referred to a set of visual phenomena of a viewer seeing some
 161 characteristics of the human visual system’s internal organization as “subjective vision”—presently,

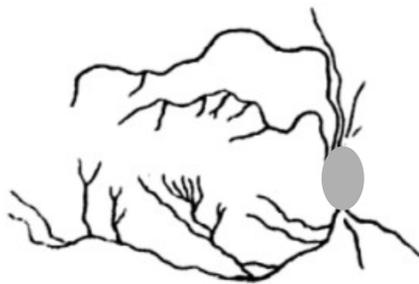
162
163
164
165
166
167
168
169
170
171
172
173
174
175
176
177
178
179
180
181
182
183
184
185
186
187
188
189
190
191
192
193
194
195
196
197
198
199
200
201
202
203
204
205
206
207
208
209
210
211
212
213
214
215



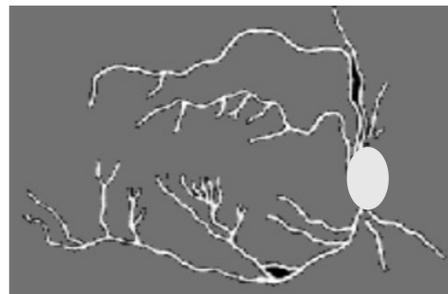
(a) The retina of a human eye as seen by an ophthalmologist with an eye / retina imaging device. Optic Disk = Blind Spot (BS); the image of retinal blood vessels: Purkinje Tree (PT). The knowledge about the optic disk and blood vessels in the human eye has been available since 1853 (see Appendix A).



(b) Mariotte's demonstration of the BS: The subject (viewer) closes their left eye and fix their right eye on the cross; as they moves closer to or farther from the image, they will experience the eye icon falling into the right eye's BS and disappearing from their view. Presently, this demonstration is universally present in all the textbooks related to human vision; but this is only one side of the BS: It is not yet actually seeing the BS. As remarked by von Helmholtz, this demonstration negatively proves the existence of the BS.



(c) The other side of the BS is that the viewer actually sees the BS in visual consciousness. This is positively proves the existence of the BS. Here, the subject sees their own eye's BS & PT in a positive form.



(d) Basically the same as in (c), but here the subject sees their own eye's BS & PT in a negative form (i.e., as a negative / complementary afterimage).

Figure 1: The blind spot and blood vessels within a human eye as seen by ophthalmologist from outside and by the subject (the owner of the eye) in entopic vision.

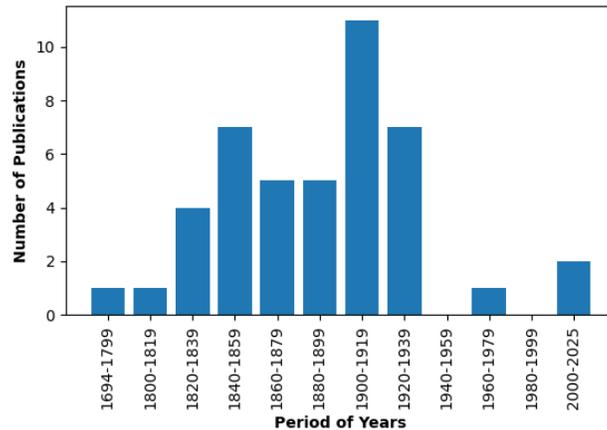


Figure 2: Numbers of Publications about the La Hire—Purkinje Phenomenon Over Periods of Years (based on the reference data presented in Appendix B).

they are known as “entoptic vision”; therefore, this La Hire—Purkinje phenomenon about seeing one’s own blind spots is an instance of entoptic vision.

As mentioned by Helson (1929, pp. 352–353) and Brøns (1939, Ch. IV), many German psychologists had investigated the La Hire—Purkinje phenomenon before World War II. After the war, very unfortunately, it appears that the vision research community has essentially forgotten about this interesting visual phenomenon: Figure 2 shows the number of publications since La Hire’s discovery in 1694; from this data plot, it is apparent that the phenomenon has largely been in oblivion after Brøns (1939, Ch. IV) (i.e., right around World War II). Recently, quite accidentally, we rediscovered this phenomenon: As soon as we experienced it, we realized its significance—as we will show below, this phenomenon can be used to precisely determine the neural locus of short-term memory. In this regard, we have been attempting to revive this visual phenomenon: We have recently presented our observations in scientific conference, and the presentation has been published as an abstract in the conference’s booklet (for anonymity, we will add its URL in the final version if our paper is accepted).

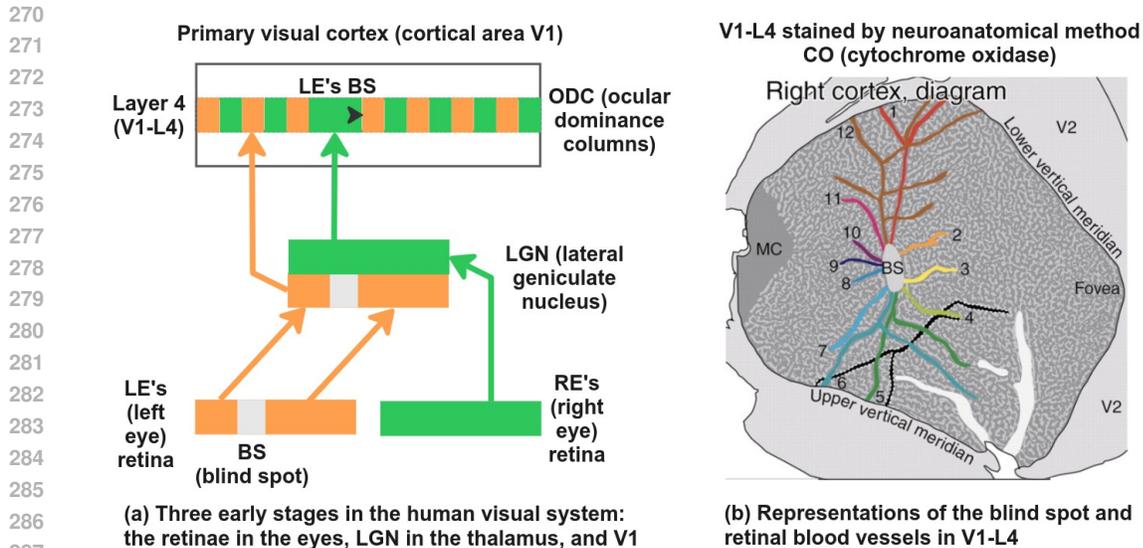
2.2 SEEING THE BLIND SPOT AS A NEGATIVE AFTERIMAGE

As a sub-phenomenon of the La Hire, we observed seeing an eye’s blind spot as a negative afterimage—that is, normally, the blind spot would appear as a black spot on a neutral background; but under special conditions, as illustrated in Figure 1(d), it may appear negatively as a brighter spot on a darker background. Actually, both Helson (1929) and Brøns (1939) had mentioned the possibility of seeing the blind spot as a negative afterimage: In this respect, on the phenomenological side, here again, our observation is a rediscovery; nonetheless, we will correlate this sub-phenomenon with some relevant neuroanatomical studies to determine the neural locus of afterimages: We will describe this correlational reasoning in detail below.

2.3 LOCALIZING THE NEURAL SUBSTRATE OF THE BLIND SPOT AND ITS AFTERIMAGE

Figure 3(a) illustrates the early stages of the human (or more broadly, the primate) visual system consisting of the retina, the lateral geniculate nucleus (LGN) of the thalamus, and the primary visual cortex (i.e., V1). The cortical sheet comprises six layers, with Layer 4 receiving thalamic inputs (i.e., optic radiations in the case of V1). Hereafter, we will denote this layer as V1-L4. Please note that “Layer 4” in V1 has been incorrectly labeled as “Layer 4C” in many textbooks (e.g., Wolfe et al., 2021, pp. 71); see Boyd et al. (2000) and Balaram et al. (2014) for the relevant neuroanatomical evidence as to why it should be labeled as “Layer 4” instead of “Layer 4C”.

The La Hire—Purkinje phenomenon is a wonderful psycho-anatomical means: As a matter of fact, several neuroanatomical studies have precisely localized a representation of the blind spot in V1-



289 Figure 3: Three early stages of the human visual system: retina, LGN, and V1-L4.

290
291
292 L4: Levay et al. (1985) and Adams et al. (2007) are the two milestone discoveries in this regard,
293 with the first one in the macaque monkey's brain and the second in the human brain. Though in
294 two species and using different chemical staining methods, their central findings are essentially the
295 same: There is a representation of the blind spot in V1-L4. For better illustration, Figure 2(b) shows
296 a diagram of V1-L4 from a monkey's brain studied by Prof. Horton's lab. Please note that V1-L4 is
297 a "bi-monocular" structure in the sense that for each and every tiny patch of the viewer's binocular
298 visual field, the monocular image (i.e., ocular dominance column or ODC in abbreviation) from
299 one eye resides, side by side, with that for the other eye. In Figure 3(b), white stripes and areas
300 depict neural tissue regions in V1-L4 predominantly connected with the eye containing the blind
301 spot, whereas the black stripes and areas depict that connected with the other. From this diagram,
302 we should understand that the representation of the blind spot in V1-L4 does not create any physical
303 "hole" in this neural tissue—instead, the area is invaded and occupied by the input from the other
304 eye.

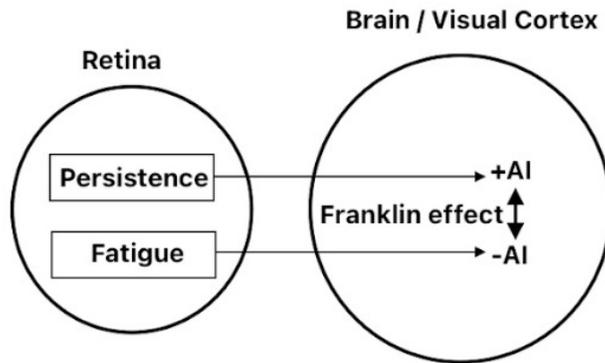
305 Beyond V1-L4, is there any other neural structure(s) in the primate visual system that may contain
306 representations of the blind spot? David Hubel and Torsten Wiesel's pioneering exploration of
307 the feline and the primate visual brains had long established that neurons in V1-L4 are primarily
308 monocular whereas that beyond V1-L4 are mainly binocular (e.g., Hubel & Wiesel, 1968). As we
309 already stated, each eye's blind spot is specific to that eye (i.e., monocular); therefore, the answer to
310 this question is negative. Correlating the La Hire phenomenon with such neuroanatomical studies,
311 we can conclude that visual sensation is represented in V1-L4. Please note that without knowing
312 the La Hire phenomenon, we cannot argue that the blind spot representations seen in V1-L4, and
313 this layer in general, are directly correlated with visual sensations and afterimages—in other words,
314 one may argue that such representations are just for sub-consciousness neural activation. With the
315 knowledge of the La Hire phenomenon, then, we can indeed pinpoint the neural substrate for visual
316 sensations and afterimages to V1-L4. Please note that the authors of the relevant neuroanatomical
317 studies did not link their findings with any visual phenomenon; here for first time, we are making
318 this critical correlation between the afterimage phenomenon and its neuroanatomical underpinning.

319 3 POSITIVE AND NEGATIVE AFTERIMAGES

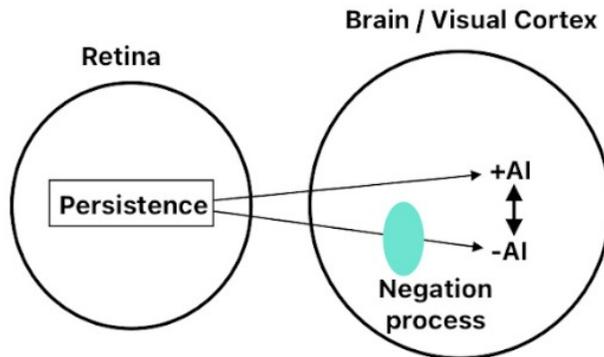
320 3.1 THE FRANKLIN EFFECT

321
322
323 One conceptual blocker to thinking of afterimages as a form of memory is that an afterimage can
manifest itself as a positive or negative one. Presently, the prevailing conception about positive and

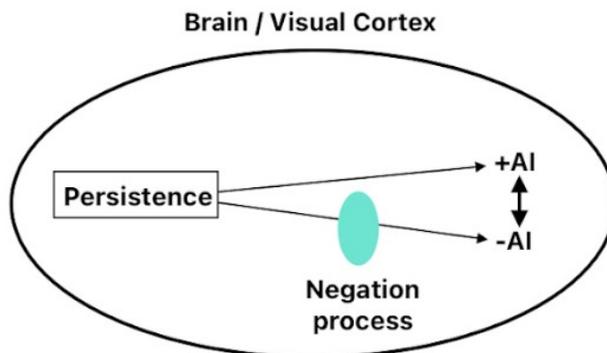
324
325
326
327
328
329
330
331
332
333
334
335
336
337
338
339
340
341
342
343
344
345
346
347
348
349
350
351
352
353
354
355
356
357
358
359
360
361
362
363
364
365
366
367
368
369
370
371
372
373
374
375
376
377



(a) Currently prevailing view:
+AI and -AI have separate
physiological processes in the retina
(e.g., Gregory, 2004, p.15);
however, this view cannot
explain the Franklin effect.



(b) McDougall's View:
+AI and -AI share the same
persistence process in the retina
(McDougall, 1901b, p.365)



(c) The view advanced in this paper:
+AI and -AI share the same
persistence / memory process
in the brain / visual cortex.

Figure 4: Three views regarding positive and negative afterimages

negative afterimages is that they are due to different physiological causes. For instance, De Valois & De Valois (1997) suggested that positive afterimages is due to temporary persistence of discharges of ganglion neurons in the retina, whereas negative afterimages is partly due to retinal photopigment bleaching and partly due to neural adaptation at an opponent-colors stage. Likewise, Gregory (2004, p. 15) presents essentially the same conception about positive and negative afterimages. The conception that positive and negative afterimages are due to separate physiological processes (or mechanisms) is schematically illustrated in Figure 4(a).

This above conception, however, is just a misconception—this is because positive and negative afterimages can be mutually converted into one another; more specifically, an afterimage can appear either positive or negative depending on whether the observer is viewing it with his/her eyes closed or open; and with the eyes open, depending on whether projecting the afterimage onto a dark, gray, or white background. This phenomenon was first observed and described by Benjamin Franklin (1706—1790) [whose life was simply too many-splendored: a founding father of the United States, a successful businessman, a scientist famous for taking electricity from the sky, and an inventor]. On June 2, 1765, in a letter to Lord Kames, Franklin described his following observation: “A remarkable circumstance attending this experiment, is, that the impression of forms is better retained than that of colors; for after the eyes are shut, when you first discern the image of the window, the panes appear dark, and the cross bars of the sashes, with the window frames and walls, appear white or bright; but, if you still add to the darkness in the eyes by covering them with your hand, the reverse instantly takes place, the panes appear luminous and the cross bars dark. And by removing the hand they are again reversed.” (Franklin, 1765, p. 380). This phenomenon had been further studied by Robert Waring Darwin (1766—1848), the father of the evolutionist Charles Darwin (1809—1882). On March 23, 1786, Darwin read a paper on “ocular spectra” (that was the term for afterimages at that time) before the Royal Society of London; the paper was subsequently published as Darwin & Darwin (1786).

The above phenomenon has been named the Franklin effect (Roeckelein, 2006, p. 649)—but to a large extent, somehow unfortunately, it remains largely unknown besides being mentioned in some comprehensively and meticulously compiled works, such as those by Roeckelein. As illustrated in Figure 4(a), the hypothesis that positive and negative afterimages are due to different physiological processes cannot account for the Franklin effect; therefore, we would need to seek other explanations for positive and negative afterimages.

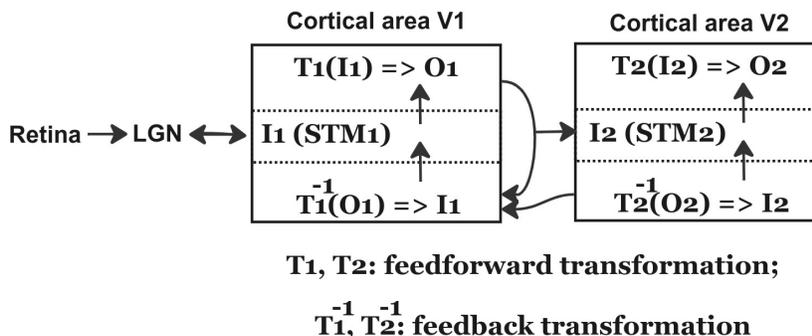
3.2 MCDUGALL’S VIEW REGARDING POSITIVE AND NEGATIVE AFTERIMAGES

One and a quarter centuries after Franklin and Darwin, Mcdougall (1901a) rediscovered the Frank effect, and then he further claimed: “...all afterimages, negative and positive, same-colored and complementary-colored alike, are primarily due to the persistence in the retina of X-substances ...” Mcdougall (1901b, p. 365). As illustrated in Figure 4(b), his claim consists of two parts: (1) positive and negative afterimages are both due to some material persistence in our visual system; (2) this persistence resides in the retina of the eye. In the previous section, however, we have already dismissed afterimage’s retinal origin; therefore, we can now adopt McDougall’s view about positive and negative afterimages and modify it to become the view illustrated in Figure 4(c).

4 AFTERIMAGES AS VISUAL SHORT-TERM MEMORY (STM)

Now we have established two facts: afterimage is cortical in origin, and positive and negative afterimages are both due to neural persistence. In our opinion, a neural persistence process (or mechanism) in the brain should better be conceived as visual STM—as a matter of fact, an elementary form of this view had already been suggested by Newton in 1704.

During the years 1661—1664, when Newton was an undergraduate student at Trinity College, he kept a notebook which has passed down in history and is currently in archive at University of Cambridge Library (see Mcdougall, 1901b). The notebook contains a section under the heading “some philosophical questions”—there, Newton wrote down a wide range of observations and questions in natural philosophy, some of them belonging to perceptual and cognitive psychology as we know today, within the topics ranging from vision, audition, memory, imagery, to consciousness. For vision, he recorded a number of visual phenomena: One of them is a particular form of positive afterimages,



445 Figure 5: The Computational Architecture of Multiple Cortical Areas in the Human Brain.

446
447
448 as he described in this way: “There is required some permanency in the object to perfect vision, thus
449 a coale whirled round is not like a coale but fiery circle . . .” (McGuire & Tamny, 1983, p. 387).
450 About 40 years later, when Newton (1704) published his book “Opticks”, he did compile this visual
451 phenomenon as one of the queries appended near the end of the book: “Query 16: . . . And when a
452 Coal of Fire moved nimble in the circumference of a Circle, make the whole circumference appear
453 like a Circle of Fire; is it not because the Motion excited in the bottom of the Eye by the Rays of
454 Light are of a lasting nature, and continue till the Coal of Fire in going round returns to its former
455 place?” (McGuire & Tamny, 1983, p. 237)

456 What Newton was describing as “permanency” in his Trinity College notebook and as “lasting na-
457 ture” in his book “Opticks” happens within the observer’s mind—apparently, it is a form of memory
458 in the human brain. Furthermore, Newton did point out that this form of positive afterimages plays
459 an active functional role in color perception—specifically, in temporal color summation (also known
460 as color mixture or color fusion)—see “Persistence of Vision” on Wikipedia (2025).

461 Now, once we understand that afterimages play an active computational role in human vision, we
462 should conceptualize afterimages better as STM rather than merely as some peripheral adaptation;
463 then, once we understand that the input layer (i.e., L4; also known as, the middle layer of the cortex)
464 in a cortical area plays the role of STM, we can easily understand the computational architecture of
465 this cortical area. As the six-layer organization is a general feature of the whole human brain, we can
466 easily understand how multiple cortical areas work together: Figure 5 illustrates the computational
467 architecture of the brain conceptualized in this manner.

468 469 470 5 CONCLUSIONS

471
472
473 Currently, the standard textbook teaching about afterimages is that they origin in the retina of the
474 eye. Here we have presented an array of evidence—particularly the phenomenon of an eye’s blind
475 spot visible as an afterimage—to argue for the cortical origin of afterimages. Furthermore, we have
476 developed a new theoretical perspective for understanding afterimages in human vision, consisting
477 of the following tenets: 1. Positive and negative afterimages share the same neural substrate; 2.
478 Afterimages should be viewed as short-term memory (STM) in the brain—rather than as peripheral
479 adaptation; 3. In terms of the neural computational architecture of the brain, this STM is sandwiched
480 between a feedforward neural network and a feedback counterpart. This work is significant towards
481 a complete understanding of the human brain’s computational mechanisms.

482 ICLR is a great venue for interdisciplinary interactions between cognitive science & neuroscience
483 on the one hand and computer science & engineering on the other. Our paper belongs to the for-
484 mer—hopefully, it would attract some talents and efforts from the latter to tackle the scientific issues
485 raised here in one direction and to transfer and incorporate some of our ideas proposed here into real-
world applications in the other.

486
487
488
489
490
491
492
493
494
495
496
497
498
499
500
501
502
503
504
505
506
507
508
509
510
511
512
513
514
515
516
517
518
519
520
521
522
523
524
525
526
527
528
529
530
531
532
533
534
535
536
537
538
539

ACKNOWLEDGMENTS

This section will be completed only for the final version.

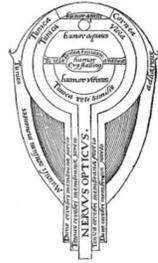
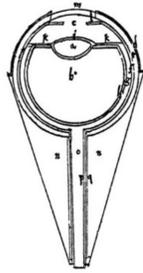
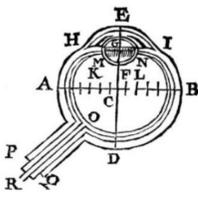
REFERENCES

- 540
541
542 Daniel L. Adams, Lawrence C. Sincich, and Jonathan C. Horton. Complete pattern of ocular domi-
543 nance columns in human primary visual cortex. *Journal of Neuroscience*, 27:10391–10403, 2007.
- 544 Pooja Balaram, Nicole A. Young, and Jon H. Kaas. Histological features of layers and sublayers in
545 cortical visual areas v1 and v2 of chimpanzees, macaque monkeys, and humans. *Eye and Brain*,
546 6:5–18, 2014.
- 547 Alfred Binet. *La psychologie du raisonnement: Recherches expérimentales par l’hypnotisme*. Félix
548 Alcan, 1886.
- 549
550 Jamie D. Boyd, Julie A. Mavity-Hudson, and Vivien A. Casagrande. The connections of layer 4
551 subdivisions in the primary visual cortex (v1) of the owl monkey. *Cerebral Cortex*, 10:644–662,
552 2000.
- 553
554 Burtis B. Breese. On inhibition. *Psychological Monograph*, 3(1):1–65, 1899.
- 555 J. Brøns. *The Blind Spot of Mariotte: Its Ordinary Imperceptibility or Filling-in and Its Facultative*
556 *Visibility*. H. K. Lewis & Co, 1939.
- 557
558 K. J. W. Craik. Origin of visual after-images. *Nature*, 145:512–512, 1940.
- 559 Robert W. Darwin and Erasmus Darwin. New experiments on the ocular spectra of light and colours.
560 *Philosophical Transactions of the Royal Society of London*, 76:313–348, December 1786.
- 561
562 Russell L. De Valois and Karen K. De Valois. Neural coding of color. In Alex Byrne and David R.
563 Hilbert (eds.), *Readings on Color—Vol. 2: The Science of Color*, volume 2, pp. 94–140. MIT
564 Press, Cambridge, MA, 1997.
- 565 Edmund B. Delabarre. On the seat of optical after-images. *The American Journal of Psychology*, 2
566 (2):326, February 1889.
- 567
568 Bo Dong, Linus Holm, and Min Bao. Cortical mechanisms for afterimage formation: evidence from
569 interocular grouping. *Scientific Reports*, 7(1), January 2017.
- 570 Benjamin Franklin. Letter to lord kames. In Albert H. Smyth (ed.), *The Writings of Benjamin*
571 *Franklin: Volume IX (edited and printed in 1906)*, pp. 1783–1788. Haskell House, Benjamin
572 Franklin, 1765.
- 573
574 Richard L. Gregory. *Oxford Companion to the Mind*. Oxford University Press, Oxford, 2004.
- 575 Harry Helson. The effects of direct stimulation of the blind spot. *The American Journal of Psychol-*
576 *ogy*, 41:345–397, 1929.
- 577
578 David H. Hubel and N. Wiesel, Torsten. Receptive fields and functional architecture of monkey
579 striate cortex. *Journal of Physiology*, 195:215–243, 1968.
- 580 Milan Ivanišević. First look into the eye. *European Journal of Ophthalmology*, 29(6):685–688,
581 2018.
- 582
583 N. Kittikiatkumjorn, W. Phusuwan, A. Sena, A. Kasemsantitham, and S. Chunamchai. Color after-
584 image is based on the color you perceive rather than the actual color of the object. In *Abstracts of*
585 *the 25th Annual Meeting of the Vision Science Society (VSS)*. VSS, 2025.
- 586 Sharif I. Kronemer, Micah Holness, A. Tyler Morgan, Joshua B. Teves, Javier Gonzalez-Castillo,
587 Daniel A. Handwerker, and Peter A. Bandettini. Visual imagery vividness correlates with after-
588 image conscious perception. *Neuroscience of Consciousness*, 2024(1):niae032, August 2024.
- 589
590 Simon Levay, M. Connolly, J. Houde, and David C. Van Essen. The complete pattern of ocular
591 dominance stripes in the striate cortex and visual field of the macaque monkey. *Journal of Neu-*
592 *roscience*, 5:486–501, 1985.
- 593 Jack M. Loomis. The photopigment bleaching hypothesis of complementary after-images: a psy-
chophysical test. *Vision Research*, 12:1587–1594, 1972.

- 594 William Mcdougall. Some new observations in support of thomas young’s theory of light and color-
595 vision: Part I. *Mind*, 10:52–97, 1901a.
596
- 597 William Mcdougall. Some new observations in support of thomas young’s theory of light and color-
598 vision: Part III. *Mind*, 10:347–382, 1901b.
599
- 600 J. E. McGuire and Martin Tamny. *Certain Philosophical Questions: Newton’s Trinity Notebook*.
601 Cambridge University Press, 1983.
602
- 602 Isaac Newton. Letter to john locke. In H. W. Turnbull (ed.), *The Correspondence of Isaac Newton:*
603 *Vol. III: 1688–1694 (edited and published in 1961)*. Cambridge University Press, 1691.
604
- 604 Isaac Newton. *Opticks: or, A Treatise of the Reflections, Refractions, Inflexions and Colours of*
605 *Light*. Sam. Smith and Ben. Walford, 1704.
606
- 607 Stephen E. Palmer. *Vision Science: Photons to Phenomenology*. The MIT Press, 1999.
608
- 608 C. Reeves and D. Taylor. A history of the optic nerve and its diseases. *Eye*, 18(11):1096–1109,
609 2004.
610
- 611 Jon E. Roewecklein. *Elsevier’s Dictionary of Psychological Theories*. Elsevier, 2006.
612
- 612 Steven K. Shevell, Rebecca St Clair, and Sang Wook Hong. Misbinding of color to form in afterim-
613 ages. *Visual Neuroscience*, 25(3):355–360, May 2008.
614
- 615 Shinsuke Shimojo, Yukiyasu Kamitani, and Shin’ya Nishida. Afterimage of perceptually filled-in
616 surface. *Science*, 293:1677–1680, 2001.
617
- 617 Naotsugu Tsuchiya and Christof Koch. Continuous flash suppression reduces negative afterimages.
618 *Nature Neuroscience*, 8(8):1096–1101, August 2005.
619
- 620 Martin J. Urist. Afterimages and ocular proprioception. *American Medical Association Archives of*
621 *Ophthalmology*, 160:161–163, 1958.
622
- 622 Nicholas J. Wade. Helmholtz at 200. *I-Perception*, 12(4):1–19, 2021.
623
- 624 Nicholas J. Wade and Josef Brožek. *Purkinje’s vision: The dawning of neuroscience*. Lawrence
625 Erlbaum Associates Publishers, 2001.
626
- 626 Lawrence Weiskrantz. An unusual case of after-imagery following fixation of an “imaginary” visual
627 pattern. *Quarterly Journal of Experimental Psychology*, 2(4):170–175, December 1950.
628
- 629 Wikipedia. Persistence of vision — Wikipedia, the free encyclopedia. [http://en.wikipedia.](http://en.wikipedia.org/w/index.php?title=Persistence%20of%20vision&oldid=1300466150)
630 [org/w/index.php?title=Persistence%20of%20vision&oldid=1300466150](http://en.wikipedia.org/w/index.php?title=Persistence%20of%20vision&oldid=1300466150),
631 2025. [Online; accessed 24-September-2025].
632
- 632 Jeremy Wolfe, Keith Kluender, Denis Levi, Linda Bartoshuk, Rachel Herz, Roberta Klatzky, and
633 Daniel Merfeld. *Sensation and Perception (6th Ed.)*. Oxford University Press, 2021.
634
- 635 Qasim Zaidi, Robert Ennis, Dingcai Cao, and Barry Lee. Neural locus of color afterimages. *Current*
636 *Biology*, 22(3):220–224, February 2012.
637
638
639
640
641
642
643
644
645
646
647

A APPENDIX A. A BRIEF HISTORY OF THE ANATOMY AND ENTOPIC VISION OF THE HUMAN RETINA

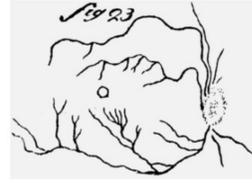
The following table lists important discoveries concerning the human retina. These contributions have been classified into two types: Anatomical / medical studies (marked with blue bullets) involve the investigators dissecting and/or looking at people's retinas, whereas vision studies (marked with green bullets) involve the investigators perceptually mapping or seeing their own eyes' blind spots and/or retinal blood vessels.

Investigator (Years of lifetime) Year of discovery/invention	Description of the investigator's contribution	Important drawing by the investigator
Galen (129–c.216)	<ul style="list-style-type: none"> Description of the optic nerve attaching to the eye (see Reeves and Taylor, 2004). 	
Hunain ibn Ishaq (c.809–c.873)	<ul style="list-style-type: none"> Preservation and translation of ancient Greek writings (see Reeves and Taylor, 2004). 	
Ibn al-Haitham (aka Alhazen, c. 965–c.1038)	<ul style="list-style-type: none"> Preservation and translation of ancient Greek writings (see Reeves and Taylor, 2004). 	
Andreas Vesalius (1515–1564) 1543	<ul style="list-style-type: none"> Meticulous drawings of the human body, including the eye (see Reeves and Taylor, 2004). 	
Christoph Scheiner (1575–1650) 1652	<ul style="list-style-type: none"> Correct illustration of the off-axis location of the optic disc, providing a giant's shoulder for Mariotte's discovery of the blind spot (see Reeves and Taylor, 2004). 	
Mariotte, E. (1620–1684) 1668	<ul style="list-style-type: none"> Discovery of the blind spot in each eye by mapping it in the observer's visual field (see Wade and Brožek, 2001). 	
La Hire, P. de (1640–1718) 1694	<ul style="list-style-type: none"> Discovery of the entoptic vision of the blood spot and retinal blood vessels with a rapid-adaptation-change procedure (see Wade and Brožek, 2001). 	

702
703
704
705
706
707
708
709
710
711
712
713
714
715
716
717
718
719
720
721
722
723
724
725
726
727
728
729
730
731
732
733
734
735
736
737
738
739
740
741
742
743
744
745
746
747
748
749
750
751
752
753
754
755

Purkinje, J. E. (1787–1869)
1819

● Discovery of the entoptic vision of the blood spot and retinal blood vessels with more experimental procedures (see Wade and Brožek, 2001).



Helmholtz, H. von
(1821–1894)
1851

● Invention of the ophthalmoscope so that a doctor can carefully examine another person's eye (see Wade, 2021).

Trigt, A. van (1825–1864)
1853

● The first known of an eye in a living human being, with the optic disc (blind spot) and retinal blood vessels clearly delineated (see Ivanišević, 2018).



● denotes an anatomic / medical investigation;

● denotes a vision / perceptual investigation;

Note: All the images included in this table were published before 1929 and therefore are already in the public domain.

References used in this table are Ivanišević (2018), Reeves & Taylor (2004), Wade (2021), and Wade & Brožek (2001).

B APPENDIX B. ORIGINAL AND IMPORTANT PUBLICATIONS ABOUT THE LA HIRE—PURKINJE ENTOPTIC VISUAL PHENOMENON

The table below lists the original and important publications about the La Hire–Purkinje Phenomenon: They were used to generate the data graph in Figure 2. Here “original publications” denote those that contain original observations and/or experimental data, and “important publications” refer to review articles that mention the phenomenon and discuss its significance. This table does not include review articles merely mentioning the phenomenon.

The authors of the present paper rediscovered the La Hire–Purkinje phenomenon in a recent year and subsequently presented their own observations at a scientific conference: The presentation has been published as an abstract in the conference’s booklet and is here listed as the last entry in the table below—It will be de-anonymized if the present paper is accepted by ICLR2026.

Author / Investigator	Publication	Type
La Hire, P. de (1694)	Dissertation sur les differens accidens de la vuë.	First report with the adaptation procedure
Purkinje, P. (1819)	Beiträge zur Kenntniss des Sehens in subjektiver Hinsicht.	Doctoral dissertation: Rediscovery with many procedures and own observations
Le Conte, J. L. (1890)	On a curious visual phenomenon.	Rediscovery with own observations
Helson, H. (1929).	The effects of direct stimulation of the blind-spot.	Important review
Brøns, J. (1939)	The Blind Spot of Mariotte: Its Ordinary Imperceptibility or Filling-in and Its Facultative Visibility.	Monograph: important review

810
811
812
813
814
815
816
817
818
819
820
821
822
823
824
825
826
827
828
829
830
831
832
833
834
835
836
837
838
839
840
841
842
843
844
845
846
847
848
849
850
851
852
853
854
855
856
857
858
859
860
861
862
863

Purkinje, P. (1823)		Original research reviewed
Purkinje, P. (1825)		by Brøns (1939)
Purkinje, P. (1830)		
Brewster, D. (1833)		
Müller, J. (1840)		
Volkman, A. W. (1846)		
Hannover, A. (1852)		
Czermak, J. (1854)		
Müller, H. (1854)		
Czermak, J. (1855)		
Aubert, H. (1865)		
Helmholtz, H. von (1867)		
Woinow, M. (1869)		
Dubrunfant (1871)		
Aubert, H. (1876)		
Charpentier, A. (1886)		
Finkelstein, L. (1894)		
Zehender, W. (1895)		
Tschermak, A. (1903)		
Tschermak, A. (1905)		
Brückner, A. (1909)		
Brückner, A. (1910)		
Brückner, A. (1911)		
Köllner, H. (1912)		
Köllner, H. (1916)		
Ebbecke, U. (1920)		
Holm, E. (1922)		
Hofmann, F. B. (1925)		
Tschermak, A. (1925)		
Pearce, I. (1968)	Entoptic visualization and impletion of the blind spot.	Original research
Pau, H. (2000)	Last but not least.	Rediscovery with own observations
The present authors	anonymized for ICLR2026 submission	Rediscovery with own observations
