out to be another relic pointing to the RNA world.

Step back in time

The very first ribozyme making copies of itself in a protocell would have been a crucial breakthrough in the evolution of life on Earth. By expanding its library of templates, it would have started the evolution of both a genome and a functional collection of ribozymes, leading towards a catalysed metabolism. Recreating this moment in the lab appears possible now and will be a momentous breakthrough in our understanding of life on Earth.

But there is still one step further back in time that needs elucidating. How did the very first polymerase ribozyme, the very first biocatalyst of any description, come into existence? By definition, it must have arisen by non-enzymatic processes from its building blocks, the ribonucleotides, or something similar. Between the simple organic compounds that formed by themselves under prebiotic conditions, as represented by the famous prebiotic chemistry experiments Stanley Miller (1930–2007) performed in the 1950s, and the first biocatalyst, there is still a gap to bridge.

Making ribonucleotides in the way a chemist would synthesise them in the lab, by attaching ribose and phosphates to the relevant base, doesn’t work in prebiotic conditions, a fact that has troubled origin-of-life researchers for many years. For the pyrimidines (C and U), the group of John Sutherland, then at the University of Manchester, UK, described an elegant alternative route creating the sugar and nucleobase simultaneously and using the phosphate as a catalyst, but for the purines (A and G) the problem persists.

In 2018, Seohyun Chris Kim in Szostak’s team discovered that inosine (I) works well in non-enzymatic RNA synthesis and could have been the precursor of guanosine in the early set of nucleotides leading to the evolution of RNA (Proc. Natl. Acad. Sci. USA (2018) *115*, 13318–13323). Inosine is readily obtained from adenosine through deamination, like U can accidentally form from C, which is the presumed reason for the use of T in DNA. Thus, assuming that I was the original member of the set and was replaced for the same reason as U was later left behind by DNA, the remaining challenge is reduced to just one nucleotide — researchers will only have to find a plausibly prebiotic way of producing adenosine.

In October 2019, the group of Thomas Carell at LMU Munich reported a prebiotic path to produce both pyrimidine and purine nucleotides, using cycles between wet and dry conditions (Science (2019) *366*, 76–82). Unlike Sutherland’s synthesis, this route is non-specific for the sugar incorporated, leaving the possibility that there was a range of similar compounds available for the synthesis of the first biopolymers. Therefore, Kim, Szostak and colleagues examined a range of plausible alternative nucleotides including arabinonucleotides and 2’deoxyribonucleotides (as used in DNA) and found that they are less efficient in non-enzymatic RNA synthesis starting from an oligonucleotide primer (J. Am. Chem. Soc. (2020) *142*, 2317–2326). The authors conclude that, among a diversity of building blocks available in prebiotic conditions, random polymerisation could have produced hybrid forms, but that template-guided polymerisation favoured those that led towards the evolution of RNA.

Back to the start

In 1953, Stanley Miller galvanised the world with his experiments showing the formation of amino acids from primordial soup in an apparatus designed to mimic conditions on early Earth. No equivalent experimental re-enactment of any of the subsequent steps has succeeded so far. Now, however, the chances are improving that biologists will one day be able to re-run the origin of life in the lab.

Obviously, there is no way of finding out how it really happened more than three billion years ago, but running a plausible model system is the next best thing and may give us fresh insights into how a molten rock battered by comets turned into a habitable planet teeming with life.

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Profile

Black Lives Matter: Revisiting Charles Henry Turner’s experiments on honey bee color vision

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The political wave of actions occurring in several countries following the death of George Floyd at the hands of Minneapolis police shows that times are changing dramatically in terms of how vast segments of our society perceive and respond to racism and social injustice against Black citizens. The campaign Black Lives Matter has gone mainstream and is no longer localized in the USA but has extended to several countries, inducing significant questioning of heroes, myths, and the way history and national identity have been built over decades. This movement has logically reached academia, as academic institutions reflect social structures and may reproduce and perpetuate social inequalities to different extents.

A positive revision of scientific history is being promoted, aiming at vindicating merits and findings by Black scientists unfairly forgotten in our current construction of scientific knowledge. This is the case for Charles Henry Turner (Figure 1), an African-American scientist who was a zoologist and educator known for his various contributions on the behavior of many animal species [1]. Born in Cincinnati, Ohio, in 1867, Turner was the first African American to receive a graduate degree at the University of Cincinnati and most likely the first African American to earn a PhD from the University of Chicago. He was not given a chance to join a university as a faculty member due to dominant racism and was finally appointed as a teacher in a small high school for African Americans, the Sumner High School in St. Louis. Bibliographical accounts on Turner mention that he received inappropriate pay and had a heavy teaching load at that school, and that he may have died

Figure 1. Charles Henry Turner.
Photo: Encyclopædia Britannica.

of overwork in 1923, at the age of 56 [1,2]. Yet, at the same time, adversity did not impede him performing dozens of experiments in the fields of animal behavior and entomology, producing important contributions that anticipated experimental psychology to various extents. He published 71 papers, including 3 in *Science*, and made fundamental discoveries on animal behavior.

Turner's scientific contributions

Summarizing Turner's scientific contributions here is difficult given the extent and diversity of his numerous works (for an extensive review, see [1]). He addressed topics such as comparative neuroanatomy in both vertebrates and invertebrates, arthropod taxonomy, insect behavior — with a particular focus on insect navigation — insect learning, spider behavior, audition in moths, leaf morphology in grapevines, and even civil rights. His neuroanatomical accounts of the avian [3,4] and invertebrate brains [5] emphasized his evolutionary views, for he was a fervent admirer of Darwin and Romanes, to the point that he named one of his sons Darwin Romanes Turner. In his numerous research works, he combined both laboratory work and field observations. While describing himself as a "stanch advocate of laboratory work", he argued that ignoring the spontaneous behavior of animals in their natural environments hinders rather than helps the solution of the problems of animal behavior [6]. A leading idea in many of his works was that animals do not behave purely based on taxia or tropisms but that they exhibit 'intelligent behavior', which he tried to analyze using different species and experimental paradigms for studying problem solving (e.g. [7]). In this way, he pioneered (without being necessarily credited for) cognitive views on animal behavior, which emerged in a more structured way many years later [8]. This position was particularly expressed in his multiple works on insect homing and navigation (see review in [9]), in which he provided accurate descriptions and analyses of the behavior exhibited by bees, ants, wasps, and caterpillars [10–14]. In these works, he proposed that memory was a fundamental property of the navigation strategies employed by these animals and formulated his conclusions in a way that anticipated the cognitive perspectives adopted at the end of the nineties to characterize insect behavior [15] by several decades. For instance, he concluded that "ants are much more than mere reflex machines; they are self-acting creatures guided by memories of past individual (ontogenetic) experience" [10].

These achievements contrast with the treatment that he received from academic institutions, which at that time denied him a faculty position based on racial issues that impregnated all levels of the society in which he had to live [1,2]. Precisely, his works are particularly remarkable because they were done in such adverse conditions: Turner had no access to institutional laboratory resources or libraries, no undergraduate or graduate students, and performed most of his work from the disadvantaged position (compared with scientists established in academic institutions) of a high school teacher.

Studies of honey bee color vision

An important and repeated claim [16,17] concerning Turner's work is that he may have discovered honey bee color vision, a finding that, in such a case, would have been attributed incorrectly to the Austrian physiologist and Nobel Prize-winner Karl von Frisch. Turner published a series of experiments on the capacity of bees to see colors in 1910 [18], while von Frisch's classical paper on this topic was published four years later [19]. Before this publication, von Frisch had advertised his findings in short communications (e.g. [20]) but without providing a precise account of his experiments, which were described in detail for the first time in 1914 [19].

Honey bees are indeed well known for their color vision capabilities, which were officially demonstrated by von Frisch [19] long before he discovered and decoded the dances employed by bees to report about profitable food sources [21]. Before him, several scientists suggested that bees may see colors (e.g. [22,23]). Yet, none of them provided the precise experimental evidence showing this capacity. Color vision is defined as the capacity to distinguish colored surfaces based on their different chromatic contents, independently of intensity differences [24]. Precisely what was absent in the works preceding von Frisch's experiments was the control of intensity differences, which von Frisch achieved using achromatic grey cardboards of variable intensity (Figure 2A).

Using a series of behavioral experiments, von Frisch showed that bees can be trained to associate different color cardboards with a reward of sucrose solution and that, in choosing a rewarded color, they distinguish it from different levels of achromatic grey cardboards, some of which displayed an intensity similar to that of the color trained (Figure 2A). He used 16 colored cardboards varying from violet to red and purple (as seen by humans). This method proved that bees could see the majority of his cardboards as colored surfaces, except in the case of red, which was confused with a black cardboard [19]. Later, Kühn extended the demonstration of bee color vision to the ultraviolet range using spectral lights produced by a mercury lamp. In this way, it was demonstrated that bees can see and discriminate colors in the range of 300 nm (ultraviolet) to orange-reddish (650 nm) [25].

The physiological basis for this capacity is the presence of three types of spectral photoreceptors in the honey bee retina that set the basis for their trichromatic color vision. Their sensitivity peaks are located at 344 nm in the short-wave (ultraviolet) region of the spectrum (S receptor), 436 nm in the middle-wave (blue) region (M receptor), and 544 nm in the long-wave (green) region of the spectrum (L receptor), respectively [26,27] (Figure 2B).

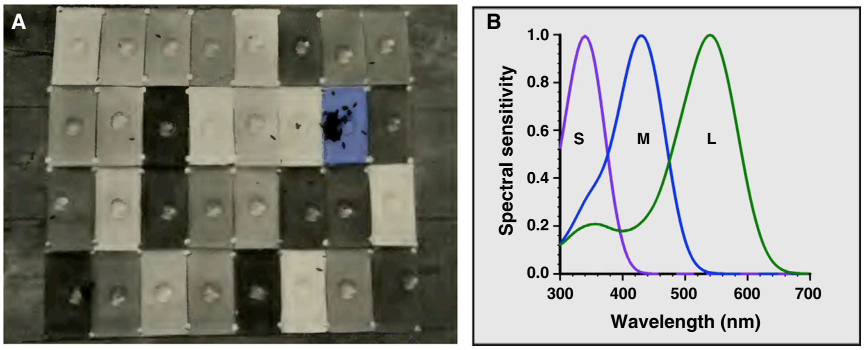
What did Turner's experiments on bee color vision show?

Four years before the appearance of von Frisch's massive work on honey bee color vision in 1914 (188 pages and 24 figures [19]), Turner published a brief account termed 'Experiments on color vision of the honey bee' (22 pages and 3 drawings [18]) where he explicitly addressed the question of whether honey bees are able to see and distinguish colors. He defined this question as "a matter of much theoretical importance for the correct interpretation of the relations of insects to flowers" [18]. The article summarized 32 brief experiments and observations performed in the field during six days (July 12th to 17th, 1910).

Two main claims have been raised with respect to von Frisch's findings and the experiments performed by Turner [16,17]. The first is a claim of priority: Turner would have made the demonstration of color vision in bees before von Frisch [1]. The second is a claim of unfairness: von Frisch would not have acknowledged Turner's findings in reporting about his own work [16].

Turner performed his experiments in the field (Figure 3) using artificial stimuli made of colored cardboards, which he placed among blossoms of *Melilotus* sp., where he detected many bees foraging at a time [18]. In all cases, when it came to attract bees to his cardboard stimuli, he baited them with honey, which he placed on the cardboards in massive quantities. Turner did not mark the bees that he was observing. He recognized that this was a limitation but argued that it was impossible to mark the many bees landing simultaneously on his stimuli individually. Yet, from his accurate behavioral descriptions, and given the short span of his experiments (six days), it is highly probable that many of the bees he observed were the same throughout his experimental series.

Turner performed three series of consecutive experiments, varying the type of stimuli used to train the bees: cardboard discs, cardboard cones, and cardboard boxes with a small opening, which allowed bees to enter to collect the honey (Figure 3). He placed his stimuli close or directly within the *Melilotus* field and tried to attract the foraging bees to them.



Current Biology

Figure 2. Honey bee color vision: von Frisch's behavioral design and the three photoreceptor types existing in the bee retina.

(A) Karl von Frisch's basic experimental design to demonstrate color vision in honey bees. Bees were trained to collect sucrose solution on a dish placed on blue cardboard. Bees chose the trained color and did not confuse it with achromatic alternatives that presented, in some cases, similar intensity. (Photo from [19].) (B) Spectral sensitivity curves of honey bee photoreceptors, peaking in the UV (S photoreceptor), blue (M photoreceptor), and green (L photoreceptor) range of the spectrum.

Importantly, and critical for the appreciation of his findings, the 'color' he chose to be associated with honey reward in his experiments was always red. Although we do not have the spectral reflection curve of the red he used, if its cardboards were standard human red, they were probably not perceived as colored by the bees. This was an unfortunate choice, but at this time Turner could not know that bees are blind to red colors. Although there is no question that bees can see such stimuli [28,29], and that they can be trained to achromatic (e.g. black) discs and patterns [30], it is probable that what he was scrutinizing was not color vision but achromatic vision. This would explain why, when he started his experiments with the red discs, and despite the presence of honey on them, bees had a difficult time detecting them.

At some point and after changing several parameters (closeness, placing the bees directly on the discs, and so on), he made the bees discover the honey; from that moment on, bees started to visit the red discs regularly and massively. In some experiments, he presented blue or green non-rewarded alternatives to prove that bees remained truthful to the red-rewarded stimuli.

After observing that bees repeatedly chose the red discs, he replaced them with red cones (Figure 3B), which were opposed to green cones. His bees went directly to the red cones containing honey, and this can be understood as a case of stimulus generalization: the bees generalized the achromatic information from the discs to the cones, which were made of the same material. Yet, the presence of honey within the cones acted as a guiding cue for the bees as shown by Turner's experiments. He offered two identical red cones, one with honey and the other without it, and found that bees almost exclusively visited the rewarded cone irrespective of its position. He then replaced these two cones with a new empty red cone and found that bees approached it but were reluctant to enter it during the first 10 minutes. Yet, they gradually entered the cone, despite the absence of honey. These observations show that bees use both visual and olfactory cues in their choice behavior. They approached the new cone, attracted by the visual cues, but in the absence of the crucial olfactory information associated with food (honey odor and eventually scent marks [31]) they rejected it, until their enhanced appetitive motivation moved them to accept it. This shows that, in most of Turner's experiments, not only visual cues but also olfactory ones were determinants.

These conclusions were verified using red rewarded boxes, sometimes opposed to green empty boxes (Figure 3C,D). Again, despite the radical change in stimulus shape, bees entered the new rewarded red boxes immediately, attracted by the visual and olfactory cues available in them. When unrewarded boxes were offered, bees first rejected them but then

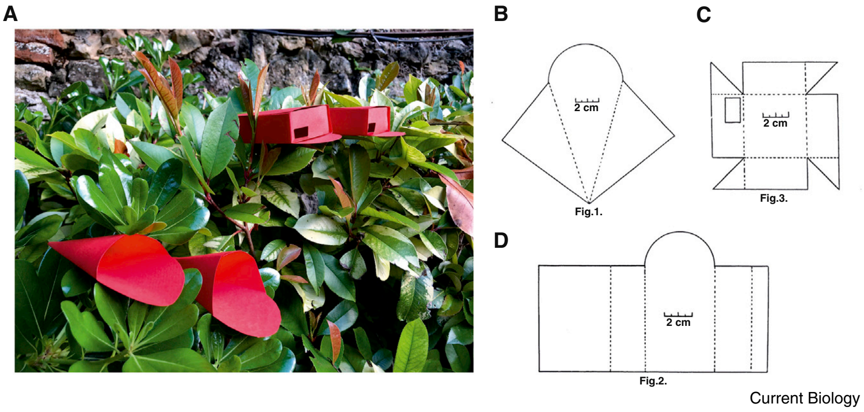


Figure 3. Turner's stimuli used to study color vision in honey bees.
(A) Real-size reconstruction of Turner's stimuli (red cones and boxes). Turner placed honey inside them to attract the bees. (B) Original description of a cornucopia provided in Turner's article. (C) Inner tray and (D) rectangular external case, which defined a box used by Turner in his experiments. Each box had a porch-like extension in front and an open end to allow accessing the tray from behind. Thanks to the accurate descriptions provided by Turner in his work, it was possible to reconstruct his stimuli in an exact way 110 years later. (Illustrations (B–D) used with permission from [18] © University of Chicago Press — Journals 1910.)

accepted them in the absence of better alternatives. Interestingly, after repeated visits to an unrewarded red box, they decided to switch to a non-rewarded green box adjacent to the red one. The switch can be explained by extinction learning — i.e. learning that the achromatic red surface was no longer rewarded — and by generalization of the shape and 3D structure of the red box to its green counterpart.

Is it thus possible to conclude that Turner demonstrated color vision in bees before von Frisch?

Not really. The choice of red as the rewarded color in all his experiments was unfortunate, but the most important point is the absence of demonstration — available in von Frisch's work — that visual-stimulus choice was unaffected by variations in the achromatic dimension of brightness. Had Turner opposed his red stimuli to black (or dark grey) ones, he may have discovered — as von Frisch did [19] — that bees confused them and thus that what he was observing was not a case of true color vision. Interestingly, Turner was aware of this problem: he explicitly wrote when discussing his findings, "whether this is a true color vision or simply a greyness discrimination is no easy question to answer". Yet, he preferred to conclude that his findings revealed true color vision based on the observation that bees preferred the red stimuli both under the sunshine and under the shadow. Clearly he was aware of the necessity of controlling this aspect, but he did not perform such a control, probably because the experiments were done under naturalistic conditions and during a very short period.

Despite the inconclusive nature of Turner's experiments on the subject of honey bee color vision, he was able to show how olfactory and visual cues guide the bees' decisions at different ranges. He demonstrated that bees were guided by visual cues at farther distances and used odor cues when they were close (a few cm) to the stimuli. More importantly, while discussing his results, he laid out principles of associative learning, which are the cornerstone of bees' foraging behavior [32]. He explained the choice of his artificial stimuli in terms of 'meaning acquisition': "those things [the stimuli] had acquired a meaning; those strange red things had come to mean 'honey bearers', and those strange green things and strange blue things had come to mean 'not-honey bearers'". This account corresponds to the Pavlovian notion of conditioned stimuli (CS) being associated with unconditioned stimuli (US) [33] and with the principle of stimulus substitution stating that the CS acquires the value of the original US as a result of conditioning [34]. Accordingly, his description of the spiraling recognition flights made by bees when leaving the rewarded stimuli after the very first visits to them as "an act by which memory pictures of the environment are formed" converged with earlier descriptions of these flights [35,36] that anticipated theories on landscape learning by bees based on visual snapshot memories by several decades [37].

It thus seems unjustified to credit Turner for the discovery of honey bee color vision, especially when comparing his experiments with the extensive work done by von Frisch. On the contrary, recognizing Turner's pioneering interpretation of honey bee foraging within an associative-learning framework is more appropriate and no less important.

Did von Frisch explicitly ignore Turner's work?

Yes and no. In his original work on honey bee color vision, von Frisch dedicated a footnote to Turner (see pages 79 and 80 in [19]). In this footnote, he wrote, "only after finishing my experiments I was noticed that Turner had performed a work, which seems to contradict at a first view my own findings". He then elaborated on Turner's findings, although surprisingly not on the ones discussed above but on a posterior work by Turner on pattern vision by bees, in which he studied the choice of colored (red-green) patterns using the boxes described above [38]. In his discussion, von Frisch focused on the spatial distribution of colors in Turner's patterns (vertical gratings vs. diagonal gratings), but he never mentioned Turner's original experiments on colors. Was he unaware of this work? Definitely not because it is listed among the references at the end of his article, together with the reference on pattern vision. However, no mention to Turner's color-vision work was made in the whole article. This is surprising, as von Frisch had no problems in discussing the experiments done by other scientists before him in his extensive contribution. The fact is, however, that he should have mentioned Turner's work on bee color vision and he did not do it. In his later book summarizing most of his productive career with a special emphasis on honey bee communication [21], no mention of Turner can be found, although the topic of color vision is covered therein (Chapter XIII).

Conclusion: a time for change

A hundred and ten years after the publication of Turner's work on honey bee color vision, society is facing a period of change in which social injustice and racism are no longer acceptable for vast segments of the population. The fact that this positive and historical turning point reaches academia can only be welcome.

Change in academia implies recognizing the merits of scientists that have been ignored, oppressed, and forgotten. It also implies recognizing that injustices are still present in the way some scientific institutions are structured and adopting a clear position against them. Our role as scientists is not only to evaluate the quality of a scientific work objectively but also to be conscious about the social conditions in which it has been produced. The decision about how to change these conditions to promote social and scientific equality is a personal one. What the current times are telling us is that there is no time for indifference.

Although in the particular case of bee color vision Charles Henry Turner cannot be credited for its discovery, reconsideration of his work allows appreciating other silenced merits, such as his analysis of honey bee foraging behavior from an associative-learning perspective, which is definitely no less important as it anticipated important notions of Pavlovian learning. His cognitive perspectives on animal behavior, infrequent at his time and in a scientific environment dominated by behaviorist views, underline his unicity and talent.

Above all, recognition of Charles Henry Turner should go beyond the frontiers of his experimental work, as what is impressive in him is the dedication devoted to his many investigations in an environment that was definitely adverse for his creativity and productivity as a scientist, to put it in mild terms. Turner's times were times in which eugenic theories were used to justify white supremacy, leading to sterilization of many African-American women during medical procedures without consent [39]. The fundamental question that will remain unanswered is what accomplishments he would have achieved if he had been given the same opportunities that white scientists had in his time. The same question should be raised today when evaluating the possibilities of minorities in academia and more generally in society.

Turner's vindication should go beyond a specific research or finding: he should be an inspiration for scientists fighting against different types of social adversity and prejudices. Initiatives such as the Charles Henry Turner Award of the Animal Behavior Society, which supports the travel to society meetings of groups traditionally under-represented in sciences, constitute a valuable step but remain modest compared with the historical reparation that is still necessary. The movement Black Lives Matter is a unique opportunity to achieve this reparation, recognize and reward 'invisible' Black scientists, and through this identify existing biases in academia for which urgent changes are needed.

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