J Comp Physiol A (2016) 202:247–266
DOI 10.1007/s00359-015-1060-1

REVIEW

Early ant trajectories: spatial behaviour before behaviourism

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Received: 10 September 2015 / Accepted: 29 November 2015 / Published online: 22 February 2016

Abstract In the beginning of the twentieth century, when Jacques Loeb's and John Watson's mechanistic view of life started to dominate animal physiology and behavioural biology, several scientists with different academic backgrounds got engaged in studying the wayfinding behaviour of ants. Largely unaffected by the scientific spirit of the time, they worked independently of each other in different countries: in Algeria, Tunisia, Spain, Switzerland and the United States of America. In the current literature on spatial cognition these early ant researchers—Victor Cornetz, Felix Santschi, Charles Turner and Rudolf Brun—are barely mentioned. Moreover, it is virtually unknown that the great neuroanatomist Santiago Ramón y Cajal had also worked on spatial orientation in ants. This general neglect is certainly due to the fact that nearly all these ant researchers were scientific loners, who did their idiosyncratic investigations outside the realm of comparative physiology, neurobiology and the behavioural sciences of the time, and published their results in French, German, and Spanish at rather inaccessible places. Even though one might argue that much of their work resulted in mainly anecdotal evidence, the conceptual approaches of these early ant researchers preempt much of the present-day discussions on spatial representation in animals.

Keywords Rudolf Brun · Victor Cornetz · Santiago Ramón y Cajal · Felix Santschi · Charles Turner

Introduction

In the history of spatial cognition in general, and ant navigation in particular, it was a lucky coincidence that at the turn from the nineteenth to the twentieth century two *Suisses Romands*, two Swiss citizens from the French speaking part of the country, moved to North Africa and stayed there for the rest of their lives (Fig. 1). They did so completely independently and never met in person. One of them—Victor Cornetz born on 17 May 1864 in Neuchâtel—worked first as a civil engineer and later as a librarian in Alger, while the other—Felix Santschi born on 1 December 1872 in Bex (Vaud)—practiced until the end of his life as a physician in Kairouan. In those days the two neighbouring North African countries Algeria and Tunisia, in which Cornetz and Santschi settled down, were governed by the French administration, which tried to attract French speaking farmers, engineers, doctors and teachers to the newly occupied territories.

Even though neither Cornetz nor Santschi were biologists by academic training, both developed a keen interest in ants, especially in *le problème du retour au nid*, in the way the ants find their way back home. This interest resulted in an abundance of observations, early field experiments and lengthy descriptive accounts published almost exclusively in French at rather inaccessible places such as the *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord*,

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Fig. 1 *Left* Victor Cornetz (1864–1936); *right* Felix Santschi (1872–1940)

Revue du Zoologie Africaine, *La Revue des Idées*, or the *Mémoires de la Société Vaudoise des Sciences Naturelles*, and hence have almost been forgotten.[1] This is unfortunate all the more as the conceptual framework within which the two researchers performed their field studies and interpreted their observations foreshadowed much of the present discussions on spatial cognition, on top-down views and bottom-up analyses. All this happened while in other parts of the world and largely unnoticed by the two Suisses in North Africa behaviourism started to dominate behavioural biology and experimental psychology. Independently of the two and of each other, a few contemporaneous scientists with different academic backgrounds also happened to get interested in the spatial orientation of ants, but the real *aficionados* in this field have been the two to whom we turn next and foremost.

In Arabian sands: Victor Cornetz and Felix Santschi

The ants' spatial behaviour

Most previous work on ant navigation had dealt with chemical orientation, especially with the much debated question whether scent trails were polarized in a directionally selective way, so that ants could discriminate between inbound and outbound directions, e.g., by the asymmetric structure of the individual trail marks.[2] As we now know, ants deduce the inbound–outbound polarity of a trail mainly from visual memories of surrounding landmarks and from the Y-shaped bifurcation structure of trail geometry rather than from polarity cues of the chemical trail itself.[3] Cornetz and Santschi, however, were not primarily interested in this debate, but focused on the orientation abilities of individually foraging ants, which navigated without the aid of chemical markers. In 1909 and 1910 Cornetz spent his summer vacations in Ain-Taya, a coastal village some 20 km east of Alger. There he recorded the trajectories of nearly 200 foraging journeys of individually searching worker ants (*les fourmis exploratrices*) belonging to several species and genera, and published most of these recordings in a special album (Fig. 2b).[4] In short, the main conclusions he drew from this collection of traces and long-winded descriptions are (a) that the ants can return to the nest only after they have actively left it, i.e., due to information obtained during the outbound journey, (b) that outbound and inbound paths do not coincide in detail, but in their general reverse direction, and (c) that in almost all cases fairly straight outbound runs are followed by circuitous searches covering a relatively extended area (*espace de recherche*), which in turn are followed by rather straight inbound runs. These results ran counter to a hypothesis proposed some years earlier by Henri Piéron, a young French researcher, who later became a famous physiological psychologist at the Collège de Fance in Paris. [5] Piéron had surmised that the ants proprioceptively recorded all movements of the legs made during an outbound journey (*sens musculaire*), memorized this sequence (*mémoire motrice*), and by replaying this program during their inbound journey were able to retrace their steps. Based on Cornetz' observations that the ants' inbound paths were not reversed copies of the outbound paths, he later abandoned this concept almost completely.

On the one hand, we now know that due to the inevitable accumulation of noise path integration can work by purely proprioceptive means only over very short distances, i.e., over much shorter distances than the ants regularly cover

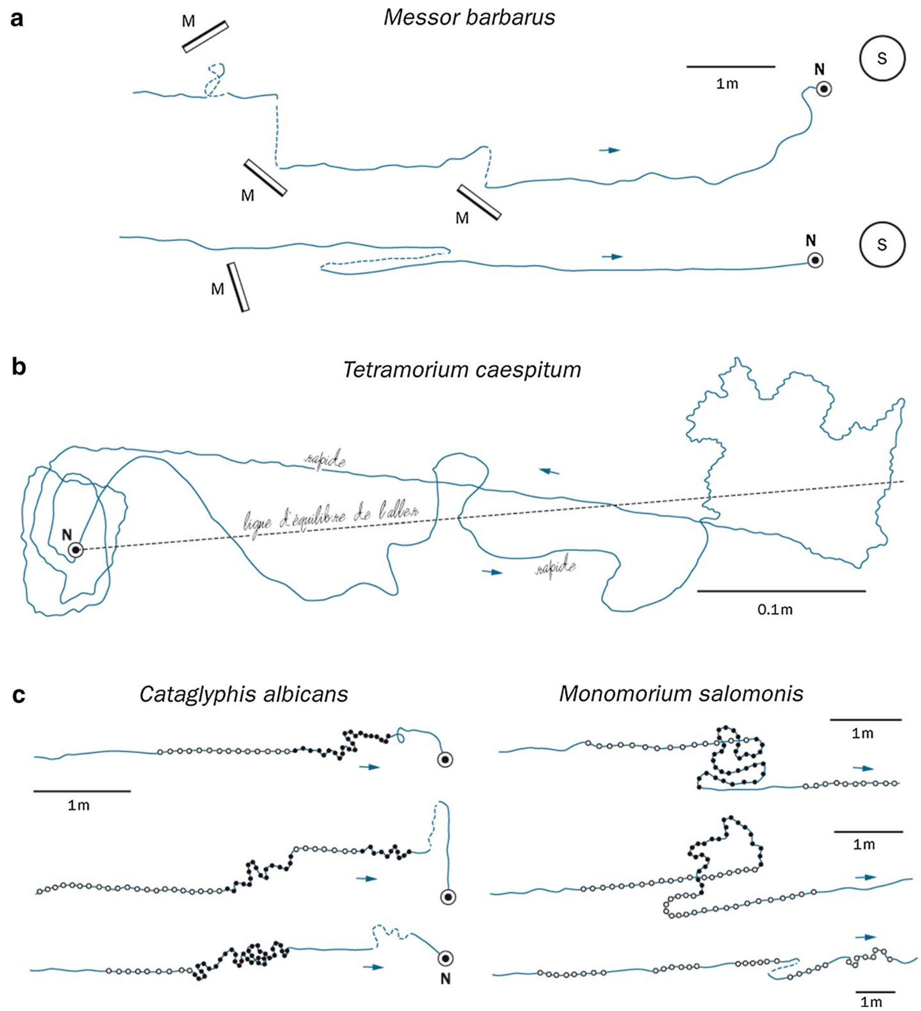

Fig. 2 Early ant trajectories as recorded by Victor Cornetz and Felix Santschi. **a** The classic mirror experiment performed during the homebound runs of two ants. The *dashed* parts of the ants' trajectories correspond to the times when the sun shade and the mirror (*M*) were put in place. *N* nest, *S* sun (Santschi 1911). **b** Record of a round-trip foraging journey (Cornetz 1910b). **c** Homeward paths recorded at or after sunset. In each case the slowly walking ant was surrounded by a cardboard cylinder, which was either open-topped (*open circles*) or covered by an opaque screen (*filled circles*) (Santschi 1923b) [Figures adapted from **a** Santschi (1911, Fig. 4), **b** Cornetz (1910b, Fig. 77), **c** Santschi (1923b, Fig. 2)]

on their foraging journeys. On the other hand, the main odometer employed by ants for gauging travel distance is a pedometer, which most likely receives its information from leg proprioceptors. Experimental evidence for the pedometer hypothesis comes from recent studies in which the lengths of the legs have been manipulated. Hence, at least in this respect, Piéron's early suggestions have been one step in the right direction.[6]

If it is not a 'motor memory' that is used to guide the ants back to their starting point, what is it then? In trying to answer this question Cornetz focussed on what he considered to be the main trait of the trajectories he had recorded: a mean direction about which all sinusoidal movements, meanderings and searches of an ant's foraging journey occurred. This was his *ligne d'equilibre d'aller*, *ligne de reference* or *l'axe de sinuement*. He realized that the ants' foraging journeys were directed rather than random walks: fairly straight trajectories finally spread out and covered an extended search area. In the meantime this directed-walk behaviour has been found to be the general space use pattern in solitarily foraging desert ants. However, as Cornetz never marked an ant individually, he could not discover the strong sector fidelity, which all desert ant species studied so far may maintain at least for part of their foraging lives.[7] He referred to Piéron's early observation that the ants kept their main inbound directions even if they were passively displaced sideways from their homebound routes (what Santschi later called *l'orientation virtuelle*), and that they repeatedly followed these routes, reversed in sign, on their subsequent foraging journeys (*conservation de l'orientation*, *la règle de constance*).[8] However, in spite of all this profligate naming in his numerous and lengthy writings—in the 5-year period of 1910–1914 alone he published 34 papers on this topic—he was never specific about the nature of the directional information that the animal actually gained and used. He vaguely referred to an "absolute internal sense of direction" (*un sens de perception des directions absolues dans l'espace*), of which he frankly admitted that he had not the slightest idea of what it could mean physiologically. It was his Swiss countryman in Tunisia, Felix Santschi, who realized on the basis of Piéron's early displacement experiments that *un sens purement* *interne*—a purely internal sense of direction—would not do, and that an external compass reference was needed (Fig. 3).[9]

By designing an ingenious experiment, Santschi was immediately successful. When he screened off the sun and reflected it with a mirror from the other side, a home-bound harvester ant, *Messor barbarus*, instantly reversed its course (Fig. 2a). To be fair, others had already shown before that *Lasius*, *Leptothorax*, and *Tapinoma* ants could use a distant light source as a compass cue.[10] However, all these former experiments had been done in the laboratory under artificial illumination conditions. Most convincingly, John Lubbock had tested *Lasius niger* while it performed its trail-bound inward journeys on a rotatable disk illuminated by a distant candle. Whenever he rotated the disk by 180°, the ants turned and ran in the counter direction. The same happened when he kept the disk stationary, but shifted the position of the light by 180°. This was the first demonstration of a visual compass in ants, and in animals in general. Historically it might be worth mentioning that like Cornetz and Santschi John Lubbock, the later Lord of Avebury, was a gentleman scientist. As the son of a wealthy banker he grew up close to Down House in Kent, where Charles Darwin lived, and thus became one of Darwin's closest young friends. It was certainly due to this early friendship with Darwin that Lubbock, who in later years became a Member of Parliament and the first President of the Institute of Bankers, got heavily engaged in entomological studies. While Cornetz and Santschi lived and practised at the fringe of the scientific world of their days, and thus remained almost unknown to the peers in their academic field, Lubbock became an eminent and well respected scholar, who received many honors and even served as Vice President of the Royal Society.

However, let us now return from Victorian England to the French protectorates in North Africa, where Santschi exposed the ants to a mirror image of the sun and hypothesized that the ant's compound eyes were 'compass eyes' designed to detect the position of the sun. When he performed some histological sections through the compound eyes of some species of desert ants, he was struck by the large amount of dark screening pigment shielding the individual retinulae (Fig. 4). Hence he thought of the ommatidial lattice as a device for localizing the position of the sun.[11] However, always a cautious experimenter, Santschi was careful enough not to over-generalize his findings by pointing out some important constraints: ants of some genera (e.g., *Messor*, *Aphaenogaster*, *Monomorium*) performed much better in the mirror experiment than others (e.g., *Cataglyphis*), and did so more readily when the sun was low and the wind had stopped blowing. Ramón y Cajal, who later tried to repeat Santschi's mirror experiments in a number of other species of ants, encountered such

Fig. 3 Envelope of a letter written by Felix Santschi to Victor Cornetz on 27 December 1910. In this letter Santschi asked whether Cornetz had any idea about the sensory basis of *la faculté de direction de la fourmi*, the ant's sense of direction, which the addressee had proposed in the same year in his "Trajets de fourmis et retours au nid" (Cornetz 1910a). Courtesy of Colette Chevrot, Saint Etienne Vallée, France

difficulties and differences as well.[12] Even though these additional experiments showed that the sun was only one component in the ant's compass system, it surely was an external reference for finding directions. We may wonder how Cornetz responded to this demonstration of a visual compass, and might be surprised to learn that he accepted it unhesitatingly. However, he relegated the visual input to an auxiliary source of information. For example he argued that displaced ants kept their courses even when they were released in the shade of an object, which he supposed to have altered the ambient light distribution substantially, or hours after they had been captured, i.e., when the sun had substantially changed its azimuthal position.[13]

In replying to these arguments Santschi performed one of his most elegant experiments and formulated one of his most far-reaching hypotheses. In one experiment he used an open-topped cardboard cylinder, by which he could present the ants with isolated sun-free patches of blue sky. Even though he studied the behaviour of only very few individuals of *Messor*, *Monomorium*, *Cataglyphis* and *Camponotus* species, he concluded that the ants could derive compass information not only from the sun, but also from blue skylight at quite some distance from the sun (Fig. 2c). Unfortunately he was unaware of the phenomenon of polarized light. When in 1947 Karl von Frisch performed a similar experiment in waggle-dancing honeybees—his 'stovepipe experiment' somehow mimicked Santschi's 'cardboard-cylinder experiment'—the bees behaved as the ants had done. Advised by two colleagues from physics departments,

Fig. 4 Felix Santschi examining histological sections under the microscope. His study room was separated only by a curtain from his medical practice in the first floor of a traditional Arab house at the Rue Ali Bel Houane in the medina of Kairouan, Tunisia. After Santschi had made some sections through the compound eyes of ants, he wondered about the thick pigment shields surrounding the individual ommatidia and concluded that as each ommatidium is looking at only one pixel of the celestial hemisphere, the compound eyes could serve as compass eyes (*les yeux boussole*). Courtesy of the late Heinrich Kutter, Flawil, Switzerland

Hans Benndorf from the University of Graz in Austria and Karl-Otto Kiepenheuer from the University of Freiburg in Germany, Karl von Frisch finally discovered that it was the polarized light in the sky that had provided the essential compass cues.[14] As to Cornetz' second reply that the sun's azimuthal position had changed considerably when the ants had been kept in the dark for some periods of time, Santschi hypothesized that a moving skymark could be as reliable as a stationary landmark if the movement were regular and predictable (as is the case with the daily movement of the sun across the sky), and if the ants had an internal representation of circadian time. Nearly half a century had to pass until these issues were taken up again,[15] and it then took some further decades until studies in skylight navigation and its neural underpinnings gathered momentum.

Dramatis personae

Why did Cornetz and Santschi differ so much in their ways of thinking about ant navigation, and why did they get engaged in such studies in the first place? Felix Santschi, the son of a paperhanger, had started his professional career as a craftsman. When he later worked as a technician in the laboratory of Eduard Bugnion, Professor of Anatomy at the University of Lausanne, he met Auguste Forel, Bugnion's brother-in-law, who by then had already become an eminent figure in both brain research and myrmecology. Bugnion and Forel recognized the young technician's intelligence and skills, and thus enabled him to acquire the degree of a Doctor of Medicine. However, as Santschi had never obtained a Swiss Grammar-School Diploma and hence had not performed the normal university studies, he was not permitted to practice as a physician in his home country. Instead he accepted an offer of the French government to work in Tunisia. There, in the holy inland city of Kairouan, where he stayed until the end of his life, he practiced as a medical doctor and performed his myrmecological studies, to which Forel had encouraged him. Actually, his fascination for ants was raised in 1896 when Santschi, then an assistant of Bugnion, joined his supervisor and Forel on an expedition led by Count Dalmas and Count de Brettes to South America.[16] Inspired by this early experience, and with Auguste Forel as his lifetime role model, Felix Santschi became an enthusiastic ant taxonomist, who ceaselessly identified, described and named an uncanny abundance of new genera, species, subspecies, races, and varieties collected by himself in North Africa or sent to him by myrmecologists from all-over the world. Unfortunately, due to his educational background and geographic isolation he was unaware of the new developments in population genetics and evolutionary biology, and hence still adhered to a typological way of thinking,[17] so that most of his taxonomic descriptions have to be reconsidered today. In the study of ant behaviour, however, Santschi took a fresh and unbiased look at old problems, and in performing some elegant field experiments was well ahead of his time, in which the 'new physiology' with its rather formalistic taxis concepts prevailed.

Victor Cornetz had a quite different educational background. He came from a well-established Neuchâtel family with several generations of doctors, scientists and local politicians. He obtained his university education at the Technical School of Karlsruhe, Germany, where he graduated as a certified engineer and subsequently became an assistant in descriptive geometry. In 1890 he moved to North Africa, where he first worked as a cartographer and geographer in southern Tunisia. Commissioned by the French administration, which had just taken possession of this part of the Ottoman Empire, he explored the largely uncharted desert areas in the 'far south' spreading from the Nefzaoua oases down to the Algerian and Libyan border at Ghadamès. During three winter seasons he traveled for months riding his camel back and forth across these remote areas, which due to the strong resistance by the local Bedouin tribes had not yet been occupied by the French military forces. Accompanied by a single Berber guide and provided with only vague topographic descriptions of the area, Cornetz collected a wealth of geographical and ethnological information and designed a detailed map, especially of the Dahar plateau and parts of the Great Eastern Erg.[18] Unlike Santschi, who very much remained a French speaking European within an

Arabic world, Cornetz dressed like a Bedouin and acquired some fluency in Arabic languages.

In hindsight it might be quite surprising that on all these travels Cornetz did not seem to have paid any attention to ants. At least in his writings there is not a single mention about any such observation. Indeed, what finally encouraged him to study ant navigation after he had settled down in Alger was neither a chance observation he had made in the Tunisian or Algerian outback nor any previous interest in ants at all, but reading Georges Bohn's *La Naissance de l'Intelligence*.[19] In those days the biological roots of intelligence had become a much debated issue, and Bohn's book was well received in the academic community. It even contained a chapter entitled *Le Problème du Retour au Nid* that dealt with the wayfinding behaviour of ants. Cornetz read this book immediately after it had appeared in 1909 and was so fascinated by it, especially by the chapter on ants, that he started his own observations straightaway. In turn, his results stimulated Santschi to perform the famous mirror experiments described above. Cornetz did not fully agree with Santschi's conclusions, Santschi fired back, and a heated debate took its course through the letters which Santschi and Cornetz exchanged from time to time (Fig. 3), but most intensively in their publications.

Given Santschi's convincing demonstration of a visual compass mechanism it is somewhat astounding that Cornetz continued to insist on the operation of a general sense of direction, which Felix Santschi and Rudolf Brun dubbed a "*faculté mystérieuse*" and "*doctrine transcendentale*".[20] One of the reasons that Cornetz failed in this respect was his obvious lack of interest in physiological mechanisms and analytical approaches. He took a more holistic stand by considering the spatial aspects of the ants' entire round-trip foraging journeys and discussing them in the light of concepts drawn from human psychology. His interest in spatial orientation in humans had already been raised in the early 1890s when he explored the remote parts of southern Tunisia and wondered about the navigational skills of his local guide from the Saharan Adari tribe.[21] Obviously he considered the ant's *directions absolues dans l'espace*, the ant's sense of direction, to be embedded in an internal map, just as he was convinced that his Adari guide referred to a mental map when he selected the right direction leading to a particular place.

In later years Cornetz often traveled from Alger to Paris, where he attended the meetings of the *Institut Général Psychologique*, and published in its bulletins. There he met the psychologist Henri Piéron, whom we have already mentioned above, and the philosopher Rémy de Gourmont, who in his famous *Promenades Philosophiques* had even referred to the "topographical sense of ants".[22] He thus mixed in intellectual circles quite different from the ones to which the myrmecologist Santschi had access in his remote retreat in central Tunisia. Cornetz considered aspects of associative learning and memory, but never rigorously applied these concepts to his own experimental design. His psychological and even philosophical interests are reflected in *L'Homme et la Fourmi*, a book which he published toward the end of his life.[23] In hindsight we may regret that Cornetz did not fully appreciate Santschi's analytical approach, and did not incorporate it in his own work. However, in spite of this failure and his partial disagreement with Santschi's conclusions he admired Santschi's "*expériences ingénieuses*" and "*simple et élégante theorie*". He even thought so highly of his colleague at Kairouan that he compared him with Auguste Forel and William Morton Wheeler, the famous myrmecologist at Harvard University.[24]

Avoiding the forced-movement trap

In their North African seclusion neither Cornetz nor Santschi participated in what could be called the foundation of behavioural physiology then developing in Europe and North America. It is against this background that Cornetz' and Santschi's approaches stand out as unique. At the forefront of the new movement in understanding the elements of behaviour was Jacques (Isaac) Loeb. During his postdoctoral time at Würzburg, Germany, he was strongly influenced by the botanist Julius Sachs. Due to this influence by the leading experimental plant physiologist of the time he compared light-directed movements of animals with tropisms of plants. This approach is well borne out by his first book written while Loeb was an assistant at the Physiological Institute of the University of Strassburg, at the very place at which Albrecht Bethe later formulated his strictly mechanistic view of animal behaviour culminating in the claim that "for biologists animal psychology does not exist".[25] When Loeb left Europe for the US, he first held positions at the University of Chicago and the University of California at Berkeley, but finally settled down at the Rockefeller Institute for Medical Research (the present-day Rockefeller University), where a new physiology department was created for him and where he became one of the most famous scientists of the country. Endowed with his "superbly penetrating intelligence", as William Crozier remarked, Loeb considered behaviour as a sequence of forced movements, of direct responses to external stimuli. Along these lines of reasoning he and many of his contemporaries and followers took a pronounced reductionist stand, which came to dominate physiological psychology in the early decades of the twentieth century.[26]

This reductionist stand had far-reaching consequences for the study of animal orientation. For example, in 1919 Alfred Kühn, then a lecturer (*Privatdozent*) at the Friedrich Wilhelm (present-day Humboldt) University in Berlin, Germany, extended and refined the concept of tropisms and taxes, which then survived in various modifications and elaborations up to the late 1960s.[27] Cornetz and Santschi did not get involved in such discussions and referred to Loeb's concept of phototropism only in passing.[28] However, Kühn later included Santschi's sun compass response in his hierarchical system of taxes and dubbed it 'menotaxis' (maintaining a given direction of movement by preserving a certain spatial distribution of sensory stimuli), but also tried to subsume it under 'mnemotaxis' (selecting a direction of movement by means of memorized sensory cues).[29] With such conceptual difficulties and formalistic extravagances the once ambitious taxis concept finally petered out. Its main shortcomings might have consisted in the fact that particular orientation responses—subcomponents of behaviour—were taken for governing the behavioural outcome as a whole.

However, such shortcomings arising from Loeb's radical reductionistic approach should not distract from the powerful influence that the work of Loeb had on the development of experimental animal physiology and the emerging field of behaviourism. On the one hand, Loeb was the leading figure in the foundation of the *Journal of General Physiology*. On the other hand, none other than John B. Watson, the father of behaviourism, who in his younger years had been one of Loeb's students, later claimed that the scientist who had exerted the greatest influence on him was Jacques Loeb. All this happened while Cornetz and Santschi were engaged in studying the homing behaviour of ants. Would they have been distracted from their novel, idiosyncratic approaches toward understanding the ants' navigational routines if they had been given the chance to leave their North African retreats and enter Loebian circles? At least Santschi was naturalist enough not to flirt too strongly with Loeb's idea of getting all life phenomena under simplistic experimental control.[30]

On the other side of the Atlantic: Charles Henry Turner

Hidden behind the curtain there was a third actor in the play *Le Retour au Nid*. Neither Cornetz nor Santschi did ever correspond with him, but they often mentioned one observation which he had made a few years before the two started their own work on ants. This third man was Charles Turner, an African American zoologist (Fig. 5), and the observation to which our North African recluses referred were small meandering search movements performed by a *Camponotus* ant, which Turner had displaced from its feeding site to an unknown place.[31] Santschi, Cornetz and Piéron later dubbed this search behaviour "*les tournoiements de Turner*" (Turner loops) or "*la recherche concentrique*" (area concentrated search). In hindsight these early references, though largely anecdotal, are the first hints at a very conspicuous navigational routine employed by ants whenever they get lost.[32] Since the early 1980s this systematic search routine has been intensively investigated especially in desert ants. These studies clearly showed that rather than moving along ever-expanding spirals the searching ants perform a series of loops increasing in size and centred about where the goal is most likely to be.[33]

Fig. 5 Charles Henry Turner (1867–1923)

Charles Henry Turner, who was born in the US two years after the end of the Civil War, can be regarded as the most significant, skillful and productive African American zoologist of his time. His many studies on insect behaviour, learning and memory stand out by their wide conceptual scope and analytical experimental approach. John B. Watson, the influential behavioural psychologist, praised Turner's "ingenious methods". According to a later remark by the entomologist Philip Rau these ingenious methods enabled Turner to "solve some of the big problems of insect behaviour".[34] All this work had to be accomplished under many handicaps, which this "thin, brown, excessively shy negro scientist" met with bravery and modesty.[35] Turner was the first African American who earned a PhD at the University of Chicago, where he had worked at the very institute at which a few years earlier Jacques Loeb had started his work in the US. Turner's dissertation paper on the homing of ants was appraised *magna cum laude*. Subsequently Turner became an extremely active and successful scientist, but due to the barrier of racism he never secured a professorship at a major American research university. After many moves as a college teacher with inadequate pay and heavy teaching loads he finally settled down at the Negro Sumner High School in St. Louis, where he stayed nearly towards the end of his life. He died in Chicago, at age 56, of "neglect and overwork", as William Burghardt Du Bois compassionately mentioned a few years after Turner's death.[36] The epithet under Charles Turner's name just reads "Scientist". However, besides having been a successful researcher, Turner was also much concerned with civil rights issues. He wrote several papers on this topic always emphasizing the preeminence of education.[37]

In the beginning of the twentieth century, when in the US animal psychology became an advancing field of research,[38] Turner was among the most analytically minded of the behavioural biologists. In reading his papers, which deal with a broad range of topics in insect behaviour, we witness and enjoy one carefully devised experiment after another performed in both the field and the laboratory. For example, in his work on colour and pattern recognition in honeybees Turner performed the first systematic training experiments to test for colour vision in these insects. When some years later Karl von Frisch did his substantial work on this subject, he mentioned Turner's paper, but remarked that he had come across it only after he had already finished his own experiments.[39] Most of Turner's field work on honeybees was done in O'Fallon Park in St. Louis, where in 1910 Turner concluded that in learning about the location of a goal the bees performed circling orientation flights during which they acquired some kind of "memory pictures" of the landmark surroundings of the goal. Drawing the same conclusion from his work on solitary bees and digger wasps, he thus raised questions that more than half a century later should become a focus of neuroethological research. Especially since the late 1970s a plethora of experimental studies on local visual homing in ants and bees as well as theoretical approaches ranging from snapshot models to image difference functions have largely confirmed Turner's general idea of memory images in insect minds.[40]

In the subtleties of experimentation we may dare say that Charles Turner was at par with, or even surpassed Felix Santschi. Moreover, he actively participated in the discussions raging at the time on 'insect intelligence'. Contradicting the Loebian and Watsonian tenets in the approaching era of behaviourism he refuted a purely 'mechanistic' view of insect behaviour and allowed for what we would now call 'cognitive' processes. This is expressed in many of his studies, especially in those on context-dependent learning in cockroaches and spatial orientation in ants, bees, and wasps.[41] In this context, it should not go unheeded that Turner was extremely well informed about the early (and especially the European) literature in animal orientation. He even complained that his American fellow scientists did not sufficiently consult the French and German contributions to this field. As the detailed references and citations in his research articles and his many reviews of the scientific literature suggest, he himself must have been able to read, and according to some anecdotal evidence also to speak, French and German.

There is yet another and even more neglected part of Turner's research: that on brain anatomy. In fact, Turner's very first paper was a thorough 100-page treatise on the morphology of the avian brain, full of anatomical detail and literature references again including many extensive German accounts. Some years later he published a comparative study on the mushroom bodies of annelids, crustaceans and insects. This work must have been substantial, because none other than William Morton Wheeler later mentioned that "in 1899 one of my students, the late Dr. C.H. Turner, published a preliminary, but no final paper on that subject", and that this paper "seems never to have been consulted by investigators of the insect brain".[42] Finally, however, we cannot end this short note on Charles Henry Turner without emphasizing one general aspect of his scientific achievements and perspectives. Based on his comparative anatomical and behavioural studies Turner became a convinced evolutionary biologist, so much so that he even named his second son Darwin Romanes Turner. One bows in awe of this highly gifted, but at present almost forgotten African American scientist.

Following in the ants' tracks: Santiago Ramón y Cajal and Rudolf Brun

At this juncture it is again worth digressing for a while from the Santschi–Cornetz debate and introducing two researchers who had been inspired by these early ant trajectories. These researchers had no personal contact either with Cornetz and Santschi or with each other, but soon after Cornetz' and Santschi's first papers had appeared they independently started their own work on ant navigation. Be it purely by chance or by some curious predestination, both had been trained—just as Santschi—in medicine and had practiced for at least some periods of their lives as physicians. One of them was none other than Santiago Ramón y Cajal, the leading neuroanatomist of his time, and perhaps of all times, and one of the most innovative thinkers in the history of the neurosciences (Fig. 6, left-hand portrait). He had already finished his monumental magnum opus, the *Textura del sistema nerviosa del hombre y vertebrados*, a two-volume, nearly 2000-page treatise on the nervous system of man and vertebrates (in 1899–1904), he had received the Nobel Price (in 1906), and he had published—together with his collaborator Domingo Sánchez y Sánchez—an amazingly beautiful and informative monograph on the visual systems of insects (in 1915),[43] before he became engaged in behavioural studies on ants (in 1918–1920). However, his interest in ants had already

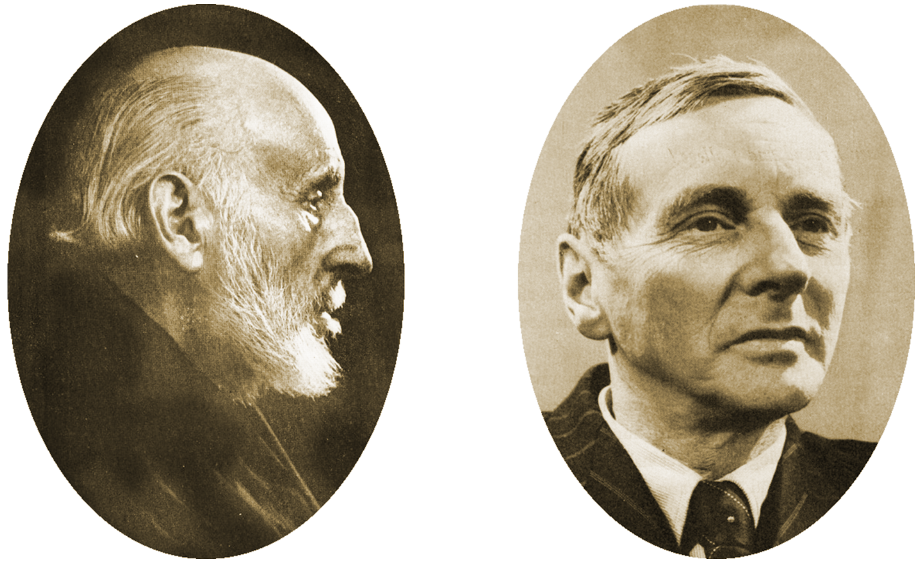

Fig. 6 *Left* Santiago Ramón y Cajal (1852–1934); *right* Rudolf Brun (1885–1969)

been raised two decades earlier by Auguste Forel. When in 1899 both scientists traveled to the US where they had been invited to present lectures and to receive honorary degrees at the Decennial Celebration of Clark University in Worcester, Massachusetts, they became friends. During their voyage on board the "La Champagne" from Le Havre to New York they had wide-ranging discussions about "everything divine and human" including "Forel's interesting studies on the psychology of ants",[44] but quite some time passed before Ramón y Cajal started his own field experiments on Forel's favorite animals. He did so only after he had retreated, during the summer months, to a rural residence north of Madrid, at Cuatro Caminos, "far from the tumult of the capital" with "splendid views towards the Moncloa, the Guadarrama, and El Escorial".[45]

As a widely read scientist Ramón y Cajal was well informed about the work not only of Cornetz and Santschi, but also of Lubbock, Forel, Wasmann, Bethe, Viehmeyer, Piéron and Turner (Fig. 7). Inspired by these authors he performed a number of experiments on olfactory, tactile, and visual orientation in a variety of ant species. In a large terrarium, which he had built especially for these experiments, he changed the near vicinity of the nest in various ways, for instance put walls and grids of differently spaced bars on the ants' habitual foraging routes. Based on the animals' behavioural responses and the numbers of ommatidia in their compound eyes he distinguished between species that relied on vision either predominantly or only weakly—between *hormigas poliópsicas* (e.g., *Formica* and *Polyergus* species) and *hormigas oligópsicas* (e.g., *Aphaenogaster* and *Tapinoma* species), respectively. Obviously he was interested more in sensory capacities than in navigational strategies, but as he has published very little about the results of his behavioural work and the conclusions derived from it,[46] we are largely left alone with a wealth of scattered handwritten notes carefully preserved in the archives of the Instituto Cajal in Madrid. There one can browse again—as in Cornetz' *Album*—through a plethora of early ant trajectories provided with short comments and excerpts from the literature, which must have been scribbled down hastily and hence are often hard to decipher.

In his work on the nervous systems of invertebrates Ramón y Cajal expressed a deep interest in the "anatomical characteristic of instinct", in the neural basis of behaviour, as we now would say. Given this interest and his painstaking anatomical analyses of the nervous systems of flies, bees, locusts, and dragonflies we may consider it a pity that neither he nor Sánchez y Sánchez, whom he later entrusted with the work on insect nervous systems, seemed to have ever made a Golgi impregnation of an ant's brain. Nearly half a century had to pass until Wolfgang Goll from the Technical University of Stuttgart-Hohenheim in Germany performed the first Golgi stainings in the nervous systems of ants (Fig. 8a).[47]

Finally, Ramón y Cajal developed a strong interest in associative learning, in the "associations with earlier impressions preserved by memory". And it is at this stage that the second of the two researchers, who were stimulated by the Cornetz–Santschi debate, comes into play, Rudolf Brun (Fig. 6, right-hand portrait). In contrast to the revered Santiago Ramón y Cajal, the "great Spaniard, scientist and prophet", as the Canadian neurosurgeon Wilder Penfield adored him,[48] Rudolf Brun is hardly known among biologists, even within the community of present-day neuroethologists working on ant navigation.[49] This is entirely unjust, as we owe to him many series of carefully conducted field and laboratory experiments on various aspects of spatial orientation in ants. In his monograph *Die Raumorientierung der Ameisen* ("Spatial Orientation in Ants")

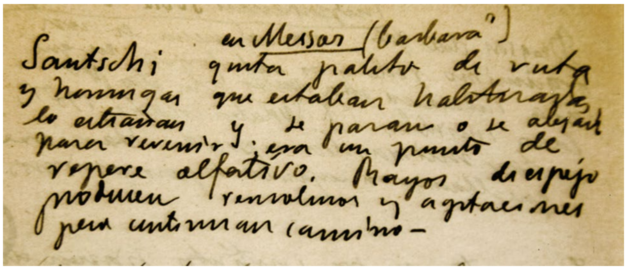
Santschi en Messor (barbara?) quita palito de ruta
y hormigas que estaban habituadas
lo extrañan y se paran o se alejan
para revenir; era un punto de
reparo olfativo. Rayos de espejo
producen remolinos y agitaciones
para continuar camino –

Fig. 7 Detail of a note written by Santiago Ramón y Cajal. Transcription: *Santschi—en Messor (barbara?)—quita palito de ruta y hormigas que estaban habituadas lo extrañan y se paran o se alejan para revenir era un punto de reparo olfativo*. *Rayos de espejo producen remolinos y agitaciones para continuar camino*. In this note Ramón y Cajal refers to two experiments performed by Santschi in *Messor barbarus*. The first leads to the assumption of some kind of olfactory reference memory. The second deals with one of Santschi's mirror experiments, in which the reflected rays of the sun disturbed the ants and caused them to get agitated, but did not prevent them from finally continuing the way. When Ramón y Cajal performed his own experiments on sensory performances in several species of ants, he finally admitted that these experiments were only preliminary ones considered as a starting point for future research. However, already being in his late sixties he did not continue this project. The handwritten note is from the Cajal archives at the Consejo Superior de Investigaciones Científicas in Madrid, Spain

published already in 1914 as well as in some later papers he dwelt on the arguments presented in the Cornetz–Santschi debate, described many own experiments performed in this context and, as a result, strongly supported Santschi's point of view.[50]

However, he gave this view an interesting new twist. Strongly influenced by Richard Semon's concept of the 'mneme', he paid special attention to the sequences of visual, olfactory and tactile memory traces, which the ants were thought to acquire and recall during their round trip journeys. Semon, a German zoologist and evolutionary biologist, who was one of Haeckel's favorite students and later a close colleague and friend of the great master at Jena, had developed a unified theory of memory formation, storage, and retrieval. Even though his 'mneme' has vaguely survived in Richard Dawkin's 'meme', in recent memory research Semon's theoretical framework has completely fallen into oblivion.[51] However, immediately after Semon's book had appeared in 1904, it was enthusiastically praised by Auguste Forel, who at this time was deeply involved in memory studies in insects and was taken by Semon's wide-ranging biological view. In turn, Forel inspired Rudolf Brun to deal with Semon's work, so that finally Brun even considered his entire research on ant navigation a contribution to the theory of the mneme—*Ein Beitrag zur Theorie der Mneme*, as the subtitle of his 1914

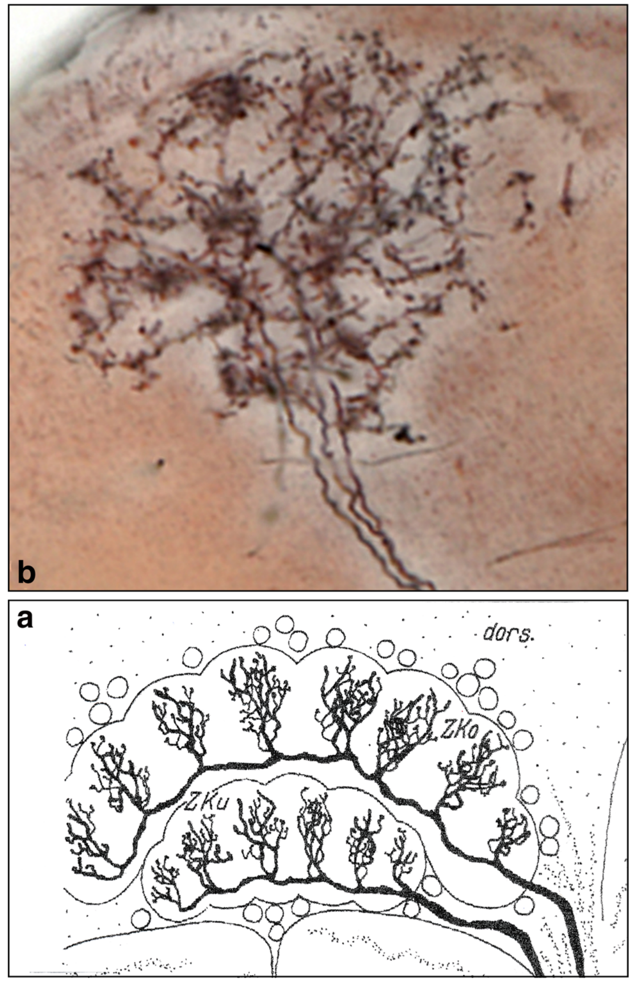

Fig. 8 **a** In 1967 Wolfgang Goll provided the first study in which Ramón y Cajal's favorite method, the silver chromate (Golgi) impregnation, was successfully applied in an ant's brain. The figure reproduces Goll's reconstruction of part of the central complex of the wood ant, *Formica rufa*. *Abbreviations* dors., dorsal; ZKo and ZKu, *Zentralkörper oberer* and *unterer Teil* (fan-shaped body and ellipsoid body), respectively. The Golgi impregnated neurons depict tangential cells of the upper and lower unit of the central complex. The tangential cell in the lower unit exhibits only six rather than the usual eight dendritic columns meaning that either the staining has been incomplete or that two lateral columns have been located in an adjacent section not used for the drawing. In their extensive work on the central complex of locusts, Uwe Homberg and his collaborators have characterized comparable neurons anatomically (e.g., by Lucifer Yellow staining) and neurophysiologically: for the tangential cells in the upper and lower unit, see Homberg (1994, Fig. 6) and Müller et al. (1997, Fig. 3), respectively. **b** Since Goll's work it was only in 1995 that Wulfila Gronenberg from the University of Arizona at Tucson succeeded in Golgi-staining neurons in the forebrain (protocerebrum) of ants. The hitherto unpublished figure depicts three Kenyon cells in the mushroom body of *Camponotus castaneus*. The Golgi impregnated neurons correspond to the "spiny lip Kenyon cells (type KI)" described by Peter G. Mobbs in honeybees (Mobbs 1982). Courtesy of Wulfila Gronenberg

monograph implies. In this monograph as well as in his later writings he interpreted the results of Cornetz' observations, Santschi's experiments and his own studies in the light of Semon's psychological perspective, and consistently used Semon's terms and concepts such as engram, engraphy and ecphory. Based on this idiosyncretic interpretation he even went so far to conclude that "the problem of the spatial orientation in ants can now be considered to be satisfactorily solved"[52]—well, for a Semonian, as we may add. However, in the present age of the neurosciences, Brun's statement will raise many an eyebrow. However, one should not belittle the intellectual and experimental rigor with which Brun performed his detailed studies on many aspects of spatial orientation in ants, even though we might search in vain for substantial discoveries transcending those of Cornetz and Santschi.

Who was Rudolf Brun? Born into a Huguenot family and grown up in the intellectually stimulating atmosphere of the liberal educational bourgeoisie (the German *Bildungsbürgertum*)—his father was a professor of art history at the Swiss Technical School (ETH) in Zürich—the young Brun attended the classical Greek-and-Latin grammar school. It was already during these years as a high school student that he developed a keen interest in entomology. Hence it did not come as a surprise that at university he first took courses in zoology. However, after two terms he turned to medicine, where he graduated under the supervision of Constantin von Monakow, one of the leading neuroanatomists and neuropathologists of his time. Having received his MD degree Brun practiced as a physician in the neurological clinic and as a Lecturer in von Monakow's Brain Anatomy Institute at the University of Zürich. He soon developed a strong interest in Freud's psychoanalysis, applied it to the treatment of his neurotic patients, and theoretically tried to give it a firm biological footing—an attempt that is clearly expressed in his main work *Allgemeine Neurosenlehre* ("General Theory of Neuroses").[53] Besides these manifold clinical activities Brun maintained a strong interest in entomology. He even started to perform comparative neuroanatomical studies of insect brains, and drew some far-reaching, though largely vague and speculative conclusions from his truly limited results. In any way, however, as a complete autodidact in insect brain research he was surprisingly well informed about the work of the great insect neuroanatomists of the second half of the nineteenth century such as Dujardin, Flögel, Viallanes, and Kenyon.[54]

An intellectual divide

With this information about Rudolf Brun and Santiago Ramón y Cajal at hand—about the two scientists who got immediately inspired by Victor Cornetz' and Felix Santschi's work—let us finally return to our North African recluses themselves. Why did they differ so much in their ways of looking at the ants' spatial behaviour? At the risk of oversimplification, let me tentatively address this question by arguing that in modern parlance Cornetz would have certainly considered himself an experimental psychologist. He favoured a top-down approach and generally adopted a cognitive stance. In contrast, Santschi, who was a more analytical thinker and a much more gifted experimentalist, focused on particular navigational routines and organized his research program in a bottom-up way.

The current discussion about spatial behaviour in social insect foragers revolves around the question of whether all information used for navigation is channelled into a central processing unit where a map-like representation of foraging space is computed, or whether the various neural modules involved in navigation interact in flexible, largely context-specific ways, so that the final decision is taken according to the salience of various external and internal factors. In a nutshell, the crucial point is whether the insect navigator relies more on positional or procedural information.[55] Even though one must be cautious in assigning scientists, who have worked a century ago in quite different intellectual environments, to present-day conceptual approaches, it might not be too far-fetched to assume that Cornetz would have taken the former position, while Santschi would have felt much closer to the latter one.

Nevertheless, in spite of their different conceptual predispositions there was at least one experimental paradigm in which Cornetz and Santschi shared their views and more or less arrived at the same conclusion. This was the detour paradigm which had been introduced by the psychologist Joseph Szymanski in a study on wood ants, and which had become known to Cornetz and Santschi by reading a paper of Georges Bohn, the professor of zoology at the Sorbonne in Paris, whom we have already mentioned above.[56] Just have a look at Fig. 9, in which the detour paradigm is sketched out. It shows how the ants' trail-bound homeward paths are obstructed by a barrier. After detouring around the obstacle, Szymanski's ants, *Formica rufa*, returned to the trail by setting a course that deviated by the angle α from the detour course. Szymanski as well as Cornetz and Santschi interpreted this behaviour as resulting from the interaction of two forces: one that immediately corrected for the enforced detour (force 1), and another one that induced the ants to continue in the former homeward direction (force 2). The turning angle α was considered to depend on the relative strengths of the two forces. Santschi, who repeated these experiments with harvester ants, *Messor barbarus*, found a large variety of intermediate courses with some ants immediately following direction 1 and the others following direction 2 for various distances before

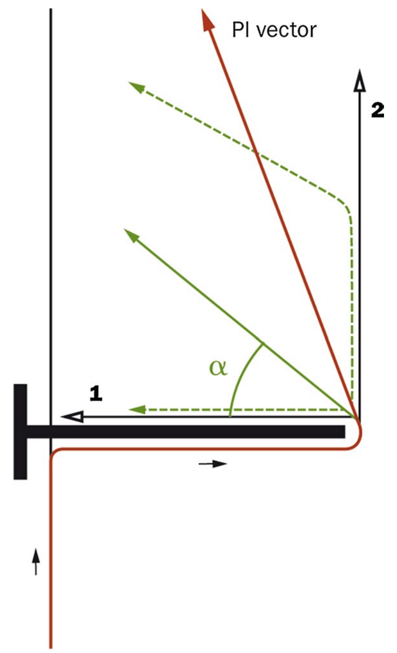

Fig. 9 Detour paradigm as designed by Joseph Szymanski in 1911. The ants are deflected by a barrier (*heavy black bar*) from their habitual homebound course (*vertical line at the left-hand side*). The ants' corrective courses observed in two classic experiments are shown in *green*. *Solid green arrow*: wood ants, *Formica rufa* (Szymanski 1911), *dashed green arrows*: harvester ants, *Messor barbarus* (Santschi 1913a, b). Szymanski as well as Cornetz and Santschi interpreted these courses as the interactive result of forces 1 and 2. The *red arrow* depicts the eventual path integration (PI) vector pointing from the end of the barrier towards the goal (nest). However, in discussing the results of the detour experiment none of the early authors considered the PI option

turning inward and rejoining the common route. He agreed with Szymanski's and Cornetz' interpretation of force 2, but attributed the inward turns (force 1) to familiar cues emanating from the common route, be these cues chemical or visual markers or even stridulatory signals produced by the nest mates marching on the trail. He further surmised that the observed variation among the individual ants was due to "psychological factors". Neither Cornetz nor Santschi, however, considered the fact that none of the detour courses seemed to have corresponded to an updated home vector course derived from path integration. In path integration (vector navigation) an animal monitors its changes in position by keeping a running total of the distance and direction that it has travelled from the starting point, and hence computes a vector pointing home. Recently path integration has become an attractive area of research in animal navigation,[57] but neither Santschi nor Cornetz took it into account. Even when Cornetz realized that the ants corrected some small sinusoidal movements around their straight outbound or inbound routes (*la marche compensée*), he did not think of path integration. Instead he argued that if ants did not follow such straight paths governed by their "innate sense of direction", *marches compensées* would not occur.[58]

However, Brun did observe that *Formica rufa* and *F. sanguinea* were able to "close the polygon" of a two-leg path, but given the landmark rich environment in which he performed his experiments he readily attributed this behaviour to the use of distant panorama cues.[59] He considered it impossible that an ant could integrate all directions steered and distances covered into a *Resultante*—"a task which even a mathematically versed human could accomplish only by tedious computations and constructions performed with pen and paper, but the ants would have to do it off the cuff".[60] Obviously, path integration was not yet a concept considered in these early studies on ant navigation.[61]

Besides the interest shown by Rudolf Brun und Santiago Ramón y Cajal, the issues which Victor Cornetz and Felix Santschi had raised, and the intellectual debate they had initiated, were scarcely recognized in wider scientific circles, then and thereafter. On the one hand, neither Cornetz nor Santschi left a single follower. On the other hand, during their lifetimes behaviourism and its particular learning paradigms were advancing rapidly,[62] and studies on more complex behavioural routines expressed by animals in their natural environments fell into oblivion. When the two almost forgotten scientists passed away—Victor Cornetz on 16 February 1936 and Felix Santschi on 20 November 1940—only a few short obituary comments appeared about the latter,[63] and none at all about the former. There was just a five-line remark hidden in a French chronicle[64] and stating that Cornetz, whose death had not become publicly known, had passed away some years ago.

Acknowledgements My biographical surveys would not have been possible without the help of several friends and colleagues, to whom I am most grateful. Colette Chevrot, Saint Etienne Vallée, France, a granddaughter of Victor Cornetz, informed me about many details of the Cornetz family. Dr. Klaus Nippert, Head of the Archives of the Karlsruhe Institute of Technology, provided me with documents relating to Cornetz' times as a student and university assistant. Over many years the late Dr. Heinrich Kutter, Flawil, Switzerland, was extremely patient in answering my many questions about Felix Santschi and Rudolf Brun, whom he had both known personally. Professor Alberto Ferrús, Director of the Cajal Institute in Madrid, Spain, kindly invited my wife and me to browse through the rich collection of Cajal's handwritten notes and manuscripts at the Instituto Cajal. Professor Charles I. Abramson (Oklahoma State University) was very helpful in discussing issues of Charles H. Turner's scientific reception. Finally my sincere thanks go to Claudia Fischer, librarian at the University of Zürich, for her invaluable help and ceaseless efforts in retrieving the necessary literature, to Wulfila Gronenberg and Uwe Homberg for anatomical information and to the former for permitting me to include Fig. 8b in this essay, to my colleague Kevan Martin for reading the manuscript and providing valuable comments, to Sarah Steinbacher for her expert help in designing the figures, to Stefan Sommer for his support in editing the manuscript, and above all to my wife Sibylle for her continuous cooperation. *Portrait credits* Victor Cornetz: courtesy of Colette Chevrot, Saint Etienne Vallée, France. Felix Santschi: courtesy of Idelette Rosa Santschi, the late daughter of Felix Santschi,

Monthey, Switzerland. Charles H. Turner: courtesy of Charles I. Abramson, Oklahoma State University, USA; published in Abramson (2009), Fig. 1. Santiago Ramón y Cajal: Ramón y Cajal (1933), frontispiece. Rudolf Brun: Minkowski and Müller (1945), frontispiece.

Notes

[1] For a biographical account written on the occasion of the 50th anniversary of Santschi's death, see Wehner (1990).

[2] At the turn of the nineteenth to the twentieth century it was a hotly discussed issue, whether trail laying ants could detect the inbound and outbound direction of a pheromone trail on the basis of the chemical polarity of the trail itself, or even of the individual footprint marks left by the marching ants, or whether they were unable to do so. Albrecht J. T. Bethe, who then was assistant at the Physiological Institute of the University of Strassburg, where a decade earlier Jacques Loeb had developed his tropism concept of animal orientation (Loeb 1890), proposed the former hypothesis (Bethe 1898, 1900, 1902). Adele Marion Fielde, an American missionary and feminist, who later in her life became a scientist, followed Bethe in this respect (Fielde 1901). Erich Wasmann, a Jesuit priest and famous entomologist, favoured the latter hypothesis (Wasmann 1898, 1901). Auguste Forel argued against either version and instead pointed out that mechanosensory information had to be taken into account as well (and in this context introduced his somewhat vague concept of a 'topochemical sense': Forel 1902, 1903). For an extensive and critical discussion of Forel's topochemical sense, see Brun (1916b). Felix Santschi later discovered by careful observation of walking ants that chemical trails did not consist of passively applied chemical footprint marks, as had previously been assumed, but by actively deposited secretions of anal glands (Santschi 1913a). Almost four decades later and unaware of Santschi's early work, John Carthy from Cambridge University 'rediscovered' this phenomenon (Carthy 1950). Finally, two more decades had to pass until the first trail pheromone of ants was chemically identified (in leafcutter ants of the genus *Atta*; Tomlinson et al. 1971).

[3] Rosengren (1971), Harrison et al. (1989) and Jackson et al. (2004).

[4] Victor Cornetz was a prolific writer. His first observations were published in the very same year in which he had started to work on ants (Cornetz 1909b). In the following year he wrote already an extensive monograph accompanied by an *Album* and lengthy handwritten notes (Cornetz 1910a, b, c).

[5] Henri Louis Charles Piéron (1881–1964) received his M.Sc. degree in philosophy and his Ph.D. degree in physiology, before he entered the field of psychology and founded, in 1920, the Institute of Psychology at the University of Paris. His work concentrated on psychophysics and comparative psychology. Much admired by his colleagues he was extremely well read as well as an active writer. While he was still working on the orientation of ants (Piéron 1912), he published his first book in psychology (Piéron 1910). Surprisingly, in his biographical essay about Piéron, Jean Piaget did not mention Piéron's myrmecological studies at all (Piaget 1966). For the classical account on Piéron's pedometer hypothesis, see Piéron (1904).

[6] For leg-manipulation studies, see Wittlinger et al. (2006). Cheung et al. provided mathematically rigorous analyses of how much noise various path integration schemes can tolerate; e.g. Cheung and Vickerstaff (2010) and Cheung (2014).

[7] Cornetz interchangeably used a number of terms depicting the marked directedness of foraging journeys, e.g. *ligne d'equilibre d'aller* (Cornetz 1910b), *ligne de reference* (Cornetz 1911a), *l'axe de sinuement* (Cornetz 1910d). For the term *espace de recherche,* see e.g. Cornetz (1910d). Since the 1980s short-term sector fidelity has been recorded in many desert ant species. For recent examples, see Muser et al. (2005) and Sommer et al. (2013).

[8] The first displacement experiments, in which ants selected homeward courses parallel to their pre-displacement courses, and ran for distances equivalent to their pre-displacement distances, were performed by Piéron (1904). Santschi dubbed this kind of orientation *l'orientation virtuelle* (Santschi 1913a). By using the terms *conservation de l'orientation* and *la règle de constance* Cornetz referred to the observation that in successive foraging runs the ants tended to maintain a rather constant direction (Cornetz 1910d, 1911b). He argued that this direction was determined by a completely internal sense of direction (*un sens de perception des directions absolues dans l'espace*; Cornetz 1914a).

[9] In an early letter to Cornetz (dated 27 December 1910) Santschi already wondered about the *faculté de direction*, which Cornetz had frankly attributed to the ants, and asked what sensory system might be involved. In his later publications he presented clear evidence against Cornetz' mysterious internal sense of direction, and instead described several ways of navigation based on a variety of external cues. His two most comprehensive accounts can be considered masterpieces of argumentation and descriptive narrative style (Santschi 1913a, 1923b).

[10] The first experiments on light compass behaviour in ants have been performed in the laboratory by John Lubbock in *Lasius* (Lubbock 1881), by Hugo Viehmeyer in *Leptothorax* (Viehmeyer 1900) and by Charles Turner in *Tapinoma* (Turner 1907). Santschi's classical 1911 paper describes the discovery of the sun compass in ants, and in fact in any animal species (Santschi 1911).

[11] Santschi (1911, 1913a). Based on considerations made by Santschi (1911, p. 324) Cornetz coined the term 'compass eyes' (*les yeux boussole*: Cornetz 1911a).

[12] Ramón y Cajal (1921); see also notes 43–46 and the special reference to Santiago Ramón y Cajal's experiments on the orientation of ants further below in the text.

[13] For Cornetz' argument about changing ambient light distributions, see Cornetz (1912, 1913a). The difficulty to account for the daily changes in solar azimuth is mentioned in Cornetz (1913b, c).

[14] Santschi published a short note on his cardboard-cylinder experiments in the very year in which he had performed them (Santschi 1914, appendix), but a detailed description followed only several years later (Santschi 1923b). There he interpreted his observation in a number of ways—for details, see Wehner (1990)—but finally was left with a riddle (Santschi 1923b, p. 159). Karl von Frisch remarked in a footnote that he had learned about Santschi's crucial experiments only after he had performed his own ones (von Frisch 1949).

[15] The paper that contains Santschi's witty remark on time compensation of the sun compass makes wonderful reading and should be a *must* for anyone interested in animal navigation (Santschi 1913a). For Santschi's rejection of Cornetz' argument by hinting at the predictability of the sun's daily movement, see also Santschi (1913b). Final proof came nearly simultaneously from experiments in bees and birds (von Frisch 1950; Kramer and von Saint Paul 1950). Before Karl von Frisch und Gustav Kramer had performed their critical experiments, the hypothesis of time compensation was erroneously refuted by Brun (1914, pp. 176–184) and Wolf (1927).

[16] The travel during which Felix Santschi accompanied Auguste Forel to South America is described at length in Forel (1935, pp. 170–187).

[17] Even though Santschi fully admired Auguste Forel and adopted nearly all of Forel's scientific, philosophical and social arguments, his taxonomic concepts show that he never became a genuine evolutionary biologist, and in this respect did not follow his master.

[18] Provided with letters of recommendation from the Swiss Ambassador in Paris and the French Minister of War to the commander of the French troops in Tunisia, Général Leclerc, Cornetz travelled at his own risk in the most southern parts of the country well beyond the French military posts in Medenine and Metameur. He stayed with the Berber tribes in the plains and sand-dune fields as well as in the rugged mountain area of the Djebel Maouaia around Guermessa and Douiret. The only geographic literature he had at hand was Largeau (1877) and Rolland (1890). His narrative report contains information not only about the physical geography and topography, but also about the distribution and life styles of the various Bedouin groups of the area (Cornetz 1897).

[19] Until 1929 Georges Bohn's *La Naissance de l'Intelligence* (The Emergence of Intelligence; Bohn 1909) was reprinted several times in French, translated into German (1910), but unfortunately never into English. For other historically interesting accounts on that subject, see Romanes (1882), Emery (1893), Wasmann (1897, 1899, 1909), von Buttel-Reepen (1900) and Lukas (1905). Much of the literature published mainly in the two decades around 1900 is discussed by Margaret Floy Washburn, then a professor of philosophy at the well renowned Vassar College north of New York City (Washburn 1908). On the early history of animal psychology, see also Claparède (1909) and Ziegler (1920).

[20] Santschi (1913a) and Brun (1916a).

[21] Cornetz (1909a). Recently, Erik Jonsson has referred to Victor Cornetz' early observations in his book "Inner Navigation": Jonsson (2002, pp. 111–116): "Adari Wayfinding in the Sahara". To the best of my knowledge this is the only time since Rudolf Brun's and Santiago Ramón y Cajal's early references that a scientist has dwelled on Victor Cornetz' work.

[22] de Gourmont (1909, pp. 153–158).

[23] Victor Cornetz wrote his final book in response to Pierre Jaccard's elaborate account on long-distance orientation in humans (Jaccard 1932; Cornetz 1933). See also Cornetz (1909a)

[24] The two appraisals of Santschi are from Cornetz (1911a, cit. p. 234; 1914b, cit. p. 9). For the comparison of Santschi with Forel and Wheeler, see Cornetz (1925, cit. p. 139).

[25] Loeb (1890). This book already foreshadowed Loeb's later attempts to consider organisms from a strictly physicochemical viewpoint. For the reference to Albrecht Bethe, see note 2.

[26] Loeb (1901, 1912, 1918), Rádl (1903) and Crozier (1929, cit. p. 48).

[27] Kühn (1919), Fraenkel (1931), Köhler (1931), Fraenkel and Gunn (1961) and Jander (1963, 1970).

[28] References to Jacques Loeb: Cornetz (1911a, p. 236) and Santschi (1913a, p. 384).

[29] For the concepts of menotaxis and mnemotaxis, see Kühn (1919, pp. 35, 51); an extended treatment has been provided by Fraenkel and Gunn (1961, pp. 106, 312).

[30] For Loeb's mechanistic conception of life, see Pauly (1987). We may add that at present the tide has turned completely. With the 'cognitive turn' in full swing, animals are regarded as autonomous agents. That sensory stimuli directly trigger behaviour—Loeb's central tenet—is now considered the exception rather than the rule, and is thought to occur mainly in emergency cases. The role of external stimuli is relegated to guiding (orienting) ongoing behaviour, and to contributing to the search process within the repertoire of behavioural modules, which the brain—the behavioural organizer—has at its disposal. This view,

which Cornetz certainly would have acknowledged, is most forcefully expressed by Heisenberg (1983, 2013). For the application of this way of thinking to homing in honeybees, see Menzel (2014).

[31] The small-scale search movements are described in Turner's Ph.D. publication (Turner 1907).

[32] Some exemplary references to the Turner loops: Cornetz (1910a), Piéron (1912) and Santschi (1913a).

[33] Wehner and Srinivasan (1981), Müller and Wehner (1994) and Schultheiss and Cheng (2011). The search loops performed around frequently visited feeding sites exhibit similar structural properties to the ones around the ants' final goal, the nest entrance (Bolek et al. 2012, Schultheiss and Cheng 2013).

[34] Watson (1907, cit. p. 300) and Rau (1923, cit. p. 290).

[35] Du Bois (1938, cit. p. 309).

[36] Du Bois' (1929) empathic "overwork" comment is certainly based on the generally acknowledged fact that Turner was an indefatigable worker during all his life, who had to perform his research under the most adverse circumstances. Turner retired from Sumner High School in St. Louis because of illness and died one year later in the house of his son in Chicago from myocarditis (Abramson et al. 2003).

[37] For biographical accounts on Charles Henry Turner, see Kessler et al. (1996), Dewsbury (2003) and Abramson (2009).

[38] Warden and Warner (1927) and Cadwallader (1984). At the turn of the nineteenth to twentieth century the University of Chicago, where Turner did his dissertation work, was among the first three academic institutions in the United States (besides Clark and Harvard), at which departments of animal psychology were established.

[39] Colour vision: Turner (1910) and von Frisch (1914; for a remark on Turner's work, see pp. 79–80). Pattern recognition: Turner (1911). In his paper on colour vision in bees Turner discussed the question of whether brightness differences could have played a role, and presented some indirect evidence that the hue of colour must have been the decisive cue, but he did not perform the finally decisive control experiments.

[40] Turner (1908a, b; 1910, cit. p. 277; 1923). For recent work on visual spatial homing in ants, see e.g. Wehner and Räber (1979), Wehner et al. (1996) and Wystrach et al. (2011, 2013). Modelling approaches range from the first formulation of the 'snapshot model' (Cartwright and Collett 1983) via concepts of 'image difference functions' (Zeil et al. 2003) to attempts of mapping the entire navigational information content of natural environments (Stürzl et al. 2015).

[41] Studies on cockroaches (Turner 1912) and hymenopterans (see notes 39, 40). William Morton Wheeler, who several times referred to Turner's work (see note 42), fully agreed with Turner's view on insect behaviour. In fact, Wheeler had "intense and heated discussions" with Jacques Loeb, when in the 1890s both were colleagues at the University of Chicago (Parker 1938, cit. p. 221). In his studies on hearing in saturniid and erebid moths Turner emphasized the functional "significance" of a stimulus necessary to elicit an animal's response (Turner 1914; Turner and Schwarz 1914). Actually, Charles Turner—together with and independently of the Slovenian zoologist Ivan Janez (Johann) Regen, who performed the famous 'telephone experiment' in crickets (Regen 1913)—provided the first conclusive behavioural evidence of hearing in insects.

[42] Turner's neuroanatomical work: Turner (1891, 1899); see Wheeler (1928, cit. p. 178). It is not clear why Wheeler called Turner one of his students. Wheeler had left the University of Chicago in 1899 for the University of Texas in Austin, and when Turner later started his studies at the University of Chicago in 1906, Wheeler was Curator of Invertebrate Zoology at the American Museum of Natural History in New York (Parker 1938; Cadwallader 1984; Abramson 2009).

[43] The pioneering accounts of Santiago Ramón y Cajal and his major collaborator Domingo Sánchez y Sánchez are timeless masterpieces in vertebrate and invertebrate neuroanatomy (Ramón y Cajal 1899–1904; Ramón y Cajal and Sánchez y Sánchez 1915). At this juncture, I invite the reader to consult Nicholas Strausfeld's brilliant account on the structure, evolution and research history of arthropod brains. In this scholarly and aesthetically appealing piece of art Nick retrieves many of the neuroanatomical treasures created by the great Spanish scientists (Strausfeld 2012).

[44] The comments are from Santiago Ramon y Cajal's autobiography (Ramón y Cajal 1937, cit. p. 485). For a published account on Forel's studies, which Ramón y Cajal later read, see Forel (1886).

[45] Ramón y Cajal (1937, cit. pp. 505 and 506).

[46] Santiago Ramón y Cajal summarized his "preliminary" data on spatial vision and orientation in ants in only one publication (Ramón y Cajal 1921). For a recent survey, see Lopera Chaves and Freire Mallo (2009).

[47] Ramón y Cajal and Sánchez y Sánchez (1915); Ramón y Cajal S (1918). In contrast to the adherents of Loeb's and Watson's mechanistic view of behaviour the contemporaneous researchers on ant navigation expressed a strong interest in the structure of insect brains, and—with the exception of Victor Cornetz—they all performed some neuroanatomical studies. The results of this work have remained largely unpublished. In this regard, it is the more regrettable that Santiago Ramón y Cajal never tried his hands at ants. The first one who did so and then succeeded beautifully was Wolfgang Goll, whom his PhD supervisor Otto Pflugfelder had introduced into using the Golgi method (Pflugfelder 1937; Goll 1967). Independently of the two researches at

Stuttgart-Hohenheim, the Golgi method was independently ‘rediscovered’ for staining individual neurons in insects by Nicholas Strausfeld, then a graduate student at University College London (Strausfeld 2012 and Fig. 3.15 therein).

[48] Reference to memory: Ramón y Cajal (1937, cit. p. 589). Wilder Penfield’s quotation is from the foreword to Ramón y Cajal’s last monograph, in which one year before his death Ramón y Cajal provided a brilliant *summa summarum* of his arguments in favour of the neuron theory, or “neuron doctrine”; see Ramón y Cajal (1933).

[49] Among biologists Rudolf Brun had been almost forgotten already at the time of his death (Kutter 1970), and in today’s community of psychologists he is completely unknown. Even though Brun was an outspoken Semonian (see notes 51, 52), Daniel Schacter does not mention him in his comprehensive account on Richard Semon (Schacter 2001). For a local appreciation of Brun’s activities as a neurologist, see Minkowski and Müller (1945).

[50] Rudolf Brun had drawn most of his conclusions from Cornetz’ and Santschi’s work and had described and discussed his own work already in an early monograph (Brun 1914). By later adding the results of new and more systematically performed experiments he refined, but did not revise his concepts expounded in *Die Raumorientierung der Ameisen.* For his later work, see Brun (1916b, 1925a, 1932). Moreover, two review papers bear witness to Brun’s comprehensive knowledge of the main topics discussed in his days in ‘animal psychology’ (Brun 1917, 1920).

[51] Richard Semon defined a ‘mneme’ in general biological terms as “the enduring though primarily latent modification in the irritable substance produced by a stimulus” (Semon 1904; English edition, cit. p. 12), as some kind of “cell or organic memory”. In Richard Dawkin’s ‘meme’ this unit of memory trace has turned into the cultural equivalent of a gene, into a unit carrying ideas, symbols or practices that can be transmitted culturally from one mind to another, and can self-replicate, mutate, and respond to selective pressures (Dawkins 1957). Surprisingly, when Dawkins introduced the term meme, he did not mention Semon’s mneme at all. The influential geneticist Wilhelm Johannsen, who had coined the term ‘gene’, read Semon’s book with interest, but concluded that even though the author had proposed some “ingenious speculations” Semon had drawn a false analogy between heredity and memory, between genes and mnemes (Johannsen 1913, cit. p. 423). Semon’s concept of the mneme was much appraised by Auguste Forel (Forel 1905). Alfred Kühn adhered to it—‘mnemotaxis’ (Kühn 1919)—but in modern memory research it has scarcely left any trace (Schacter 2001). Etymologically, the term mneme is derived from μνήμη (mnēmē), Greek for memory. Mnemosyne is the Greek goddess of memory.

[52] Brun (1914, cit. p. 17). In order to appreciate this statement one has to take into account that Brun strictly adhered to Semon’s mnemic (psychological) terminology and described all results of his studies on spatial learning in ants in the framework of Semon’s concepts (Brun 1914, pp. 25–28).

[53] Brun (1942). How Brun after having overcome some initial hesitation became a Freudian, and how he tried to reconcile psychoanalysis with his kind of biological thinking, is described in Brun (1926, 1956). See also Aeschlimann (1980).

[54] For Rudolf Brun’s neuroanatomical studies on some insect species including ants, see Brun (1923, 1925b).

[55] Two papers in *The New Visual Neurosciences* might suffice to provide an impression of the current discussion on the structure of the insect’s navigational toolkit (Menzel 2014; Wehner et al. 2014). The main views are expressed most concisely in a debate revolving around the interpretation of particular experiments in visual navigation of honeybees (Cheeseman et al. 2014 and rebuttals).

[56] Szymanski (1911), Bohn (1912) and Santschi (1913a).

[57] For detailed studies on path integration in ants, see e.g. Müller and Wehner (1988), Collett and Collett (2000) and Wehner et al. (2002); see also note 61.

[58] Cornetz (1929). This is Victor Cornetz’ last paper on spatial orientation of ants. There and in former papers he only occasionally addressed the question of what we now call path integration, but deliberately dismissed of this possibility. He concluded that the ants were incapable of *trigonométrie automatique* and instead behaved according to *la règle du contre-pied* (Cornetz 1914a, p. 118).

[59] As can be deduced from his published records, Rudolf Brun had clear evidence that *Formica* and *Polyergus* foragers referred to distant landmark cues, when they “closed the polygon” (Brun 1914, pp. 195–196, 215; Brun 1916b, pp. 300–302). Nearly a century had to pass until systematic studies showed that in cluttered, landmark-rich environments—similar to those in which Brun had performed his experiments—landmark guidance could almost completely override path integration, so that under these conditions the latter cannot be properly studied (Fukushi 2001; Beugnon et al. 2005; Narendra et al. 2013).

[60] Brun (1914, cit. p. 192). The contemporaneous neglect of path integration as a possible means of navigation is the more astounding as in marine navigation ‘dead reckoning’ had been used for centuries (Taylor 1950), and as in an early study on pigeon homing Édouard Claparède, Professor of Psychology at the University of Geneva, had already alluded to path integration in describing a bird’s ability to directly return to the home loft after displacement along a twisted detour route (Claparède 1903). For even earlier, though vague discussions of whether homing pigeons could use information obtained by route integration during their outbound journeys, see Darwin (1873), Exner (1883) and Reynaud (1898).

[61] In research on animal orientation the concept of path integration was first formalized by Horst and Marie-Luise Mittelstaedt (Mittelstaedt 1963; Mittelstaedt and Mittelstaedt 1973). As this kind of navigation results in the computation of a goal vector, it has also been treated as 'vector navigation' (Wehner 1982; Collett and Collett 2000). Full theoretical analyses of path integration have recently been provided by Allen Cheung and Robert Vickerstaff, see e.g., Cheung and Vickerstaff (2010) and Vickerstaff and Cheung (2010). In forced detour paradigms similar to the one shown in Fig. 9, *Cataglyphis* ants always update their home vector correctly (Schmidt et al. 1992; Wehner 2003 and Fig. 2b therein).

[62] Thorndike (1911), Watson (1913), Pavlov (1928) and Skinner (1938).

[63] Bulletin de la Société Entomologique Suisse 18:286–289 (1940). Entomologist's Record and Journal of Variation 53:56, 99–100 (1941). Arbeiten über morphologische und taxonomische Entomologie aus Berlin-Dahlem 8:6–7 (1941). Revista de la Sociedad Entomologica Argentina 13:344 (1947). For a biographical account on Felix Santschi, see note [1].

[64] L'Année Psychologique 38:979 (1937).

References

Abramson CI (2009) A study in inspiration: Charles Henry Turner (1867–1923) and the investigation of insect behavior. Annu Rev Entomol 54:343–359

Abramson CI, Jackson LD, Fuller CL (2003) Charles Henry Turner: significant events and unanswered questions. In: Abramson CI, Fuller CL, Jackson LD (eds) Selected papers and biography of Charles Henry Turner (1867–1923), pioneer of comparative animal behavior studies. Edwin Mellen Press, Lewiston, NY, pp 19–69

Aeschlimann J (1980) Rudolf Brun (1885–1969): Leben und Werk des Zürcher Neurologen, Psychoanalytikers und Entomologen. Zürcher Medizingesch Abh 144:1–71

Bethe A (1898) Dürfen wir den Ameisen und Bienen psychische Qualitäten zuschreiben? Pflügers Arch Ges Physiol 70:15–100 (with 2 plates)

Bethe A (1900) Noch einmal über die psychischen Qualitäten der Ameisen. Plügers Arch Ges Physiol 79:39–52

Bethe A (1902) Die Heimkehrfähigkeit der Ameisen und Bienen zum Teil nach neueren Versuchen. Eine Erwiderung auf die Angriffe von v. Buttel-Reepen und von Forel. Biol Centralbl 22:193–215, 234–238

Beugnon G, Lachaud JP, Chagné P (2005) Use of long-term stored vector information in the neotropical ant *Gigantiops destructor*. J Insect Behav 18:415–432

Bohn G (1909) La Naissance de l'Intelligence. E. Flammarion, Paris

Bohn G (1912) Les sensations et les idées-forces d'après des travaux experimentaux récents. Rev Idées 9:132–152

Bolek S, Wittlinger M, Wolf H (2012) What counts for ants: how return behaviour and food search of *Cataglyphis* ants are modified by variations in food quantity and experience. J Exp Biol 215:3218–3222

Brun R (1914) Die Raumorientierung der Ameisen und das Orientierungsproblem im allgemeinen. Eine kritisch-experimentelle Studie, zugleich ein Beitrag zur Theorie der Mneme. G. Fischer, Jena

Brun R (1916a) Le problème de l'orientation lointaine chez les fourmis et la doctrine transcendentale de V. Cornetz. Rev Suisse Zool 24:355–388

Brun R (1916b) Weitere Untersuchungen über die Fernorientierung der Ameisen. Biol Centralbl 36:261–303

Brun R (1917) Psychologie. In: Escherich K (ed) Die Ameise. 2nd edn. Vieweg, Braunschweig, pp 278–316

Brun R (1920) Das Instinktproblem im Lichte der modernen Biologie. Schweiz Arch Neurol Psychiat 6:80–124, 193–166

Brun R (1923) Vergleichende Untersuchungen über Insektengehirne, mit besonderer Berücksichtigung der pilzförmigen Körper (Corpora pedunculata Dujardini). Schweiz Arch Neurol Psychiat 13:144–172

Brun R (1925a) Experimente zur Fernorientierung der Ameisen. Mitt Schweiz Entomol Ges 13:413–416

Brun R (1925b) Ein Fall von Hirntumor bei der Ameise. Schweiz Arch Neurol Psychiat 16:86–99

Brun R (1926) Experimentelle Beiträge zur Dynamik und Ökonomie des Triebkonflikts (Biologische Parallelen zu Freuds Triebelehre). Imago. Z Anwend Psychoanalyse Natur Geisteswiss 12:147–170

Brun R (1932) Psychologische Forschungen an Ameisen. In: Abderhalden E (ed) Handbuch der biologischen Arbeitsmethoden. Abt VI: Methoden der experimentellen Psychologie. Teil D: Methoden der vergleichenden Tierpsychologie. Urban und Schwarzenberg, Berlin, pp 179–232

Brun R (1942) Allgemeine Neurosenlehre. Biologie, Psychoanalyse und Psychohygiene leib-seelischer Störungen. B Schwabe, Basel (English edition: General theory of neuroses. International University Press, New York, 1951)

Brun R (1956) Mein Weg zu Freud. Schweiz Z Psychol Anwend 15:125–130

Cadwallader TC (1984) Neglected aspects of the evolution of American comparative and animal psychology. In: Greenberg G, Tobach E (eds) Behavioral evolution and integrated levels: the TC Schneirla conference series. Erlbaum, Hillsdale, pp 15–48

Carthy JD (1950) Odour trails of *Acanthomyops fuliginosus*. Nature 166:154

Cartwright BA, Collett TS (1983) Landmark learning in bees: experiments and models. J Comp Physiol 151:521–543

Cheeseman JF, Millar CD, Greggers U, Lehmann K, Pawley MDM, Gallistel CR, Warman GR, Menzel R (2014) Way-finding in displaced clock-shifted bees proves bees use a cognitive map. PNAS 111:8949–8954 (Rebuttal by Cheung A, Collett M, Collett TS, Dewar A, Dyer F, Graham P, Mangan M, Narendra A, Philippides A, Stürzl W, Webb B, Wystrach A, Zeil J (2014) PNAS 111. doi:10.1073/pnas.1415738111. Reply by Cheeseman et al. (2014) PNAS 111, doi:10.1073/pnas.1415738111)

Cheung A (2014) Animal path integration: a model of positional uncertainty along tortuous paths. J Theor Biol 341:17–33

Cheung A, Vickerstaff R (2010) Finding the way with a noisy brain. PLoS Comput Biol 6(11):e1000992

Claparède É (1903) La faculté d'orientation lontaine (sens de direction—sens du retour). Arch Psychol 2:133–180

Claparède É (1909) Die Methoden der tierpsychologischen Beobachtungen und Versuche. In: Über Tierpsychologie. Zwei Vorträge von L. Edinger und É. Claparède. J.A. Barth, Leipzig, pp 31–67

Collett M, Collett TS (2000) How do insects use path integration for their navigation? Biol Cybern 83:245–259

Cornetz V (1897) Le Sahara Tunisien. Étude Géographique. Société de Géographique, Paris (Preprint (1896) in: Bull Soc Géogr, Sér 7, 17:518–554)

Cornetz V (1909a) Observations sur le sens de la direction chez l'homme. Rev Idées 6:60–65

Cornetz V (1909b) Le sentiment topographique chez les fourmis. Rev Idées 6:452–458

Cornetz V (1910a) Trajets de fourmis et retours au nid. Mém Inst Gén Psychol, Sect Psychol Zool 2:1–167

Cornetz V (1910b) Album faisant suite aux trajets de fourmis et retours au nid. Mém Inst Gén Psychol Sect Psychol Zool 2, plates 1–44

Cornetz V (1910c) Texte exploratif de l'album faisant suite aux trajets de fourmis et retours au nid. Inst Gén Psychol Sect Psychol Zool 2(Supp l):1–68

Cornetz V (1910d) Un règle de constance dans les trajets lointains de la fourmi exploratrice. Rev Idées 7:387–400

Cornetz V (1911a) L'œil-boussole de la fourmi d'après Santschi. Rev Idées 8:233–239

Cornetz V (1911b) La conservation de l'orientation chez la fourmi. Rev Suisse Zool 19:153–173

Cornetz V (1912) Quelques observations sur l'estimation de la distance chez la fourmi. Bull Soc Hist Nat Afr Nord 4:39–45

Cornetz V (1913a) Transport de fourmi d'un milieu dans un autre. Bull Soc Hist Nat Afr Nord 5:199–212

Cornetz V (1913b) Divergences d'interprétation à propos de l'orientation chez la fourmi. Rev Suisse Zool 21:795–806

Cornetz V (1913c) Les pistes de fourmis. La Nat 41:419–421

Cornetz V (1914a) Les Explorations et les Voyages des Fourmis. E. Flammarion, Paris

Cornetz V (1914b) Opinions diverses à propos de l'orientation chez la fourmi. Bull Soc Hist Nat Afr Nord 6:5–12

Cornetz V (1925) Un anniversaire: l'expérience de Piéron. Bull Soc Hist Nat Afr Nord 16:132–145

Cornetz V (1929) Orientation, conservation de la direction, marche compensée, polarisation. J Psychol Norm Pathol 26:354–409

Cornetz V (1933) L'Homme et la Fourmi. L'Association des Écrivains Algériens, Alger

Crozier WJ (1929) The study of living organisms. In: Murchison C (ed) The foundations of experimental psychology. Clark University Press, Worcester, pp 45–127

Darwin C (1873) Origin of certain instincts. Nature 7:417–418

Dawkins R (1957) The selfish gene. Oxford University Press, Oxford

de Gourmont R (1909) Promenades philosophiques. Mercure de France, Paris

Dewsbury DA (2003) Charles Henry Turner, scientist. In: Abramson CI, Fuller CL, Jackson LD (eds) Selected papers and biography of Charles Henry Turner (1867–1923), pioneer of comparative animal behavior studies. Edwin Mellen Press, Lewiston, pp 1–17

Du Bois WEB (1929) Postscript. The crisis, June, pp 203–204, 212

Du Bois WEB (1938) The Negro scientist. Am Scholar 8:309–320

Emery C (1893) Intelligenz und Instinkt der Tiere. Bemerkungen zu E. Wasmanns neuestem Werke: Die zusammengesetzten Nester und gemischten Kolonien der Ameisen. Biol Centralbl 13:151–155

Exner S (1883) Negative Versuchsergebnisse über das Orientierungsvermögen der Brieftauben. Sitzungsber Akad Wiss Wien Math Naturwiss Klasse 102:318–331

Fielde AM (1901) Further study of an ant. Proc Acad Sci Phila 53:521–544

Forel A (1886) Expériences et remarques critiques sur les sensations des insectes. Recl Zool Suisse 4:1–29, 145–240 [(with 1 plate). Appendix ibd. 4:515–523 (1888)]

Forel A (1902) Die psychischen Fähigkeiten der Ameisen und einiger anderer Insekten, mit einem Anhang über die Eigentümlichkeiten des Geruchssinnes bei jenen Tieren. Reinhardt, München

Forel A (1903) Nochmals Herr Bethe und die Insektenphysiologie. Biol Centralbl 23:1–3

Forel A (1905) Richard Semons Mneme als arterhaltendes Prinzip im Wechsel des organismischen Geschehens. Arch Rassen Gesellschaftsbiol 2:169–197

Forel A (1935) Rückblick auf mein Leben. Europa-Verlag, Zürich

Fraenkel GS (1931) Die Mechanik der Orientierung der Tiere im Raum. Biol Rev Cambridge Phil Soc 6:37–87

Fraenkel GS, Gunn DL (1961) The orientation of animals. Kineses, taxes and compass reactions, 2nd edn. Dover, New York

Fukushi T (2001) Homing in wood ants, *Formica japonica*: use of the skyline panorama. J Exp Biol 204:2063–2072

Goll W (1967) Strukturuntersuchungen am Gehirn von *Formica*. Z Morph Ökol Tiere 59:143–210

Harrison JF, Fewell JH, Stiller TM, Breed MD (1989) Effects of experience on use of orientation cues in the giant tropical ant. Anim Behav 37:869–871

Hartwick E, Friend W, Atwood C (1977) Trail-laying behaviour of the carpenter ant, *Camponotus pennsylvanicus* (Hymenoptera: Formicidae). Canad Entomol 109:129–136

Heisenberg M (1983) Initiale Aktivität und Willkürverhalten bei Tieren. Naturwissenschaften 70:70–78

Heisenberg M (2013) Action selection. The brain as a behavioral organizer. In: Menzel R, Benjamin PR (eds) Invertebrate Learning and Memory. Elsevier and Academic Press, Amsterdam and Boston, pp 9–13

Homberg U (1994) Flight-correlated activity changes in neurons of the lateral accessory lobes in the brain of the locust *Schistocerca gregaria*. J Comp Physiol A 175:597–610

Jaccard P (1932) Le Sens de la Direction et l'Orientation lointaine chez l'Homme. Payot, Paris

Jackson DE, Holcombe M, Ratnieks FLW (2004) Trail geometry gives polarity to ant foraging networks. Nature 432:907–909

Jander R (1963) Grundleistungen der Licht- und Schwereorientierung von Insekten. Z Vergl Physiol 47:381–430

Jander R (1970) Ein Ansatz zur modernen Elementarbeschreibung der Orientierungshandlung. Z Tierpsychol 27:771–778

Johannsen WL (1913) Elemente der exakten Erblichkeitslehre. G. Fischer, Jena

Jonsson E (2002) Inner navigation. Why we get lost and how we find our way. Scribner, New York

Kessler JH, Kidd JS, Kidd RA, Morin KA (1996) Distinguished African American scientists in the 20th century. Oryx Press, Phoenix

Klotz JH (1987) Topographic orientation in two species of ants (Hymenoptera: Formicidae). Insectes Soc 34:236–251

Köhler O (1931) Die Orientierung von Pflanze und Tier im Raum II. Biol Zentralbl 51:36–58

Kramer G, von Saint Paul U (1950) Stare lassen sich auf Himmelsrichtungen dressieren. Naturwissenschaften 37:526–527

Kühn A (1919) Die Orientierung der Tiere im Raum. G. Fischer, Jena

Kutter H (1970) In Erinnerung an Rudolf Brun. Mitt Schweiz Entomol Ges 43:68–71

Largeau V (1877) Le Sahara. Premier voyage d'exploration. Sandoz et Fischbacher, Paris

Loeb J (1890) Der Heliotropismus der Tiere und seine Übereinstimmung mit dem Heliotropismus der Pflanzen. G. Hertz, Würzburg

Loeb J (1901) Comparative Physiology of the Brain and Comparative Psychology. J. Murray, London (Extensively revised English edition of Loeb J (1899) Einleitung in die vergleichende Gehirnphysiologie und vergleichende Psychologie mit besonderer Berücksichtigung der wirbellosen Thiere. J.A. Barth, Leipzig)

Loeb J (1912) The mechanistic conception of life: biological essays. University of Chicago Press, Chicago
Loeb J (1918) Forced movements, tropisms, and animal conduct. J.B. Lippincott, Philadelphia and London
Lopera Chaves MC, Freire Mallo MA (2009) Experimentos de Santiago Ramón y Cajal sobre el comportamiento de los hormigas. Pens Psicol Revist Nac Psicol Univ Coop Colombia 5:39–45
Lubbock J (1881) Ants, bees and wasps: A record of observations on the habits of the social hymenoptera. Kegan Paul, Trench, Trubner, London
Lukas F (1905) Psychologie der niedersten Tiere. Eine Untersuchung über die ersten Spuren psychischen Lebens im Tierreiche. W. Braumüller, Wien and Leipzig
Menzel R (2014) The cognitive structure of visual navigation in honeybees. In: Werner JS, Chalupa LM (eds) The new visual neurosciences. MIT Press, Cambridge, pp 1179–1189
Minkowski M, Müller M (1945) Herrn Professor Dr. Rudolf Brun zum 60. Geburtstag. Schweiz Arch Neurol Psychiat 55:213–216
Mittelstaedt H (1963) Bikomponenten-Theorie der Orientierung. Ergeb Biol 26:253–258
Mittelstaedt H, Mittelstaedt ML (1973) Mechanismen der Orientierung ohne richtende Aussenreize. Fortschr Zool 21:46–58
Mobbs PG (1982) The brain of the honeybee *Apis mellifera*. I. The connections and spatial organization of the mushroom bodies. Philos Trans R Soc B 298:309–354
Müller M, Wehner R (1988) Path integration in desert ants, *Cataglyphis fortis*. Proc Natl Acad Sci USA 85:5287–5290
Müller M, Wehner R (1994) The hidden spiral: systematic search and path integration in desert ants, *Cataglyphis fortis*. J Comp Physiol A 175:525–530
Müller M, Homberg U, Kühn A (1997) Neuroarchitecture of the lower division of the central body in the brain of the locust (*Schistocerca gregaria*). Cell Tissue Res 288:159–176
Muser B, Sommer S, Wolf H, Wehner R (2005) Foraging ecology of the thermophilic Australian desert ant, *Melophorus bagoti*. Austr J Zool 53:301–311
Narendra A, Gourmaud S, Zeil J (2013) Mapping the navigational knowledge of individually foraging ants, *Myrmecia croslandi*. Proc R Soc B 280:20130683
Oliveira PS, Hölldobler B (1989) Orientation and communication in the neotropical ant *Odontomachus bauri* (Hymenoptera, Formicidae, Ponerinae). Ethology 83:154–166
Parker GH (1938) Biographical memoirs of William Morton Wheeler 1865–1937. Natl Acad Sci USA Biogr Mem 19:203–241
Pauly PJ (1987) Controlling life. Jacques Loeb and the engineering ideal in biology. Oxford University Press, New York and Oxford
Pavlov IP (1928) Lectures on conditioned reflexes. International Publishers, New York
Pflugfelder O (1937) Vergleichend-anatomische, experimentelle und embryologische Untersuchungen über das Nervensystem und die Sinnesorgane der Rhynchoten. Zoologica 34:1–102 (with 25 plates including 163 figures)
Piaget J (1966) Henri Piéron: 1881–1964. Am J Psychol 79:147–150
Piéron H (1904) Du rôle du sens musculaire dans l'orientation des fourmis. Bull Inst Gén Psychol 4:168–186
Piéron H (1910) L'Évolution de la Mémoire. E. Flammarion, Paris
Piéron H (1912) Le problème de l'orientation envisagé chez les fourmis. Scientia 12(Suppl):217–243
Rádl EM (1903) Untersuchungen über den Phototropismus der Tiere. W. Engelmann, Leipzig
Ramón y Cajal S (1899–1904) Textura del sistema nerviosa del hombre y vertebrados. Nicolás Moya [English edition (1995): Histology of the nervous system of man and vertebrates. Oxford University Press, New York and Oxford]
Ramón y Cajal S (1918) Observaciones sobre la estructura de los ocelos y vias nerviosas ocelares de algunos insectos. Trab Lab Invest Biol Univ Madrid 16:109–139
Ramón y Cajal S (1921) Las sensaciones de las hormigas. Arch Neurobiol Psicol Fisiol Neurol Psiquiat 2:321–337
Ramón y Cajal S (1933) Neuronismo o reticularismo? Las pruebas objectivas de la unidad anatómica de las celulas nerviosas. Arch Neurobiol 13:1–144. [Republished in English (1954): Neuron Theory or Reticular Theory? Objective Evidence of the Anatomical Unity of Nerve Cells. Consejo Superior de Investigaciones Cient, Madrid]
Ramón y Cajal S (1937) Recollections of my life. MIT Press, Cambridge
Ramón y Cajal S, Sánchez y Sánchez D (1915) Contribution al conocimiento de los centros nerviosos de los insectos. Part 1. Retina y centros opticos. Trab Lab Invest Biol Univ Madrid 13:1–168
Rau P (1923) Dr. Charles Henry Turner. Entomol News 34:289–292
Regen J (1913) Über die Anlockung des Weibchens von *Gryllus campestris* durch telephonisch übertragene Stridulationslaute des Männchens. Ein Beitrag zur Frage der Orientierung bei den Insekten. Pflügers Arch Ges Physiol 155:193–200
Reynaud C (1898) The laws of orientation among animals. Rev Deux Mond (Paris) 146:380–402
Rolland G (1890) Géologie du Sahara algérien et aperçu géologique sur le Sahara de l'Ocean Atlantique à la Mer Rouge. Imprimerie Nationale, Paris
Romanes GJ (1882) Animal intelligence. Kegan Paul, Trench and Spottiswoode, London
Rosengren R (1971) Route fidelity, visual memory and recruitment behaviour in foraging wood ants of the genus *Formica* (Hymenoptera, Formicidae). Acta Zool Fenn 133:1–106
Santschi F (1911) Observations et remarques critiques sur le mécanisme de l'orientation chez les fourmis. Rev Suisse Zool 19:305–338
Santschi F (1913a) Comment s'orientent les fourmis. Rev Suisse Zool 21:347–426
Santschi F (1913b) A propos de l'orientation virtuelle chez les fourmis. Bull Soc Hist Nat Afr Nord 5:231–235
Santschi F (1914) Première série de recherches sur l'orientation céleste des fourmis. Bull Soc Hist Nat Afr Nord 6:206–212
Santschi F (1923a) Les differentes orientations chez les fourmis. Rev Zool Afr 11:111–144
Santschi F (1923b) L'orientation sidérale des fourmis et quelques considérations sur leurs differentes possibilités d'orientation. Mém Soc Vaud Sci Nat 4:137–175
Schacter DL (2001) Forgotten ideas. Neglected pioneers. Richard Semon and the story of memory. Psychology Press, Philadelphia
Schmidt I, Collett TS, Dillier FX, Wehner R (1992) How desert ants cope with enforced detours on their way home. J Comp Physiol A 171:285–288
Schultheiss P, Cheng K (2011) Finding the nest: inbound searching behaviour in the Australian desert ant, *Melophorus bagoti*. Anim Behav 81:1031–1038
Schultheiss P, Cheng K (2013) Finding food: outbound searching behaviour in the Australian desert ant *Melophorus bagoti*. Behav Ecol 24:128–135
Semon R (1904) Die Mneme als erhaltendes Prinzip im Wechsel des organismischen Geschehens. W. Engelmann, Leipzig. [English edition (1921): The Mneme. Allen and Unwin, London]
Skinner BF (1938) The behavior of organisms. Appleton, New York
Sommer S, Weibel D, Blaser N, Furrer A, Wenzler NE, Rössler W, Wehner R (2013) Group recruitment in a thermophilic desert ant, *Ocymyrmex robustior*. J Comp Physiol A 199:711–722

Strausfeld NJ (2012) Arthropod brains. Evolution, functional elegance, and historical significance. Belknap Press of Harvard University Press, Cambridge

Stürzl W, Grixa I, Mair E, Narendra A, Zeil J (2015) Three-dimensional models of natural environments and the mapping of navigational information. J Comp Physiol A 201:563–584

Szymanski JS (1911) Ein Versuch, das Verhältnis zwischen modal verschiedenen Reizen in Zahlen auszudrücken. Pflügers Arch Ges Physiol 138:457–486

Taylor EGR (1950) Five centuries of dead reckoning. J Navig 3:280–285

Thorndike EL (1911) Animal intelligence: Experimental studies. Macmillan, New York

Tomlinson JH, Silverstein RM, Moser JC, Brownlee RG, Ruth JM (1971) Identification of the trail pheromone of a leaf-cutting ant, *Atta texana*. Nature 234:348–349

Turner CH (1891) Morphology of the avian brain. J Comp Neurol 1:39–93, 107–133, 265–286

Turner CH (1899) Notes on the mushroom bodies of the invertebrate: a preliminary paper on the comparative study of the arthropod and annelid brain. Zool Bull 2:155–160

Turner CH (1906) A preliminary note on ant behavior. Biol Bull 12:31–36

Turner CH (1907) The homing of ants: an experimental study of ant behavior. J Comp Neurol Psychol 17:367–434

Turner CH (1908a) The homing of the mud-dauber. Biol Bull 15:215–225

Turner CH (1908b) The homing of the burrowing-bees (Anthophoridae). Biol Bull 15:247–258

Turner CH (1910) Experiments on color-vision of the honey bee. Biol Bull 19:257–279

Turner CH (1911) Experiments on pattern-vision of the honey bee. Biol Bull 21:249–264

Turner CH (1912) An experimental investigation of an apparent reversal of the responses to light of the roach *Periplaneta orientalis*. Biol Bull 23:371–386

Turner CH (1914) An experimental study of the auditory powers of the giant silk worm moths (Saturniidae). Biol Bull 27:325–332

Turner CH (1923) The homing of the Hymenoptera. Trans Acad Sci St Louis 24:27–45

Turner CH, Schwarz E (1914) Auditory powess of the *Catocala* moths: an experimental field study. Biol Bull 27:275–293

Vickerstaff RJ, Cheung A (2010) Which coordinate system for modelling path integration? J Theor Biol 263:242–261

Viehmeyer H (1900) Beobachtungen über das Zurückfinden von Ameisen (*Leptothorax unifasciatus*) zu ihrem Neste. Illus Z Entomol 5:311–313

von Buttel-Reepen H (1900) Sind die Bienen Reflexmaschinen? Experimentelle Beiträge zur Biologie der Honigbiene. Biol Centralbl 20:97–109, 130–144, 177–193, 209–224, 289–304

von Frisch K (1914) Der Farbensinn und Formensinn der Biene. Zool Jb Physiol 37:1–182

von Frisch K (1949) Die Polarisation des Himmelslichts als orientierender Faktor bei den Tänzen der Bienen. Experientia 5:142–148

von Frisch K (1950) Die Sonne als Kompass im Leben der Bienen. Experientia 6:210–222

Warden CJ, Warner LH (1927) The development of animal psychology in the United States during the past three decades. Psychol Rev 34:196–205

Washburn MF (1908) The animal mind. A text-book of comparative psychology. Macmillan, New York

Wasmann E (1897) Instinct und Intelligenz im Thierreich. Ein kritischer Beitrag zur modernen Thierpsychologie. Herder'sche Verlagsbuchhandlung, Freiburg i.Br

Wasmann E (1898) Eine neue Reflextheorie des Ameisenlebens. Biol Centralbl 18:578–589

Wasmann E (1899) Die psychischen Fähigkeiten der Ameisen. Zoologica 26:1–133

Wasmann E (1901) Zum Orientierungsvermögen der Ameisen. Allg Z Entomol 6(19–21):41–43

Wasmann E (1909) Die psychischen Fähigkeiten der Ameisen. Mit einem Ausblick auf die vergleichende Tierpsychologie. Schweizerbartsche Verlagsbuchhandlung, Stuttgart

Watson JB (1907) A preliminary note on ant behavior [Review of Turner CH (1906)]. Psychol Bull 4:300–301

Watson JB (1913) Psychology as the behaviorist views it. Psychol Rev 20:158–177

Wehner R (1982) Himmelsnavigation bei Insekten. Neurophysiologie und Verhalten. Neujahrsbl Naturf Ges Zürich 184:1–132

Wehner R (1990) On the brink of introducing sensory ecology: Felix Santschi (1872–1940)—Tabib-en-Neml. Behav Ecol Sociobiol 27:295–306

Wehner R (2003) Desert ant navigation: how miniature brains solve complex tasks. J Comp Physiol A 189:579–588

Wehner R, Räber F (1979) Visual spatial memory in desert ants, *Cataglyphis bicolor* (Hymenoptera, Formicidae). Experientia 35:1569–1571

Wehner R, Srinivasan MV (1981) Searching behaviour of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). J Comp Physiol 142:325–338

Wehner R, Michel B, Antonsen P (1996) Visual navigation in insects: coupling of egocentric and geocentric information. J Exp Biol 199:129–140

Wehner R, Gallizzi K, Frei C, Vesely M (2002) Calibration processes in desert ant navigation: vector courses and systematic search. J Comp Physiol A 188:683–693

Wehner R, Cheng K, Cruse H (2014) Visual navigation strategies in insects: lessons from desert ants. In: Werner JS, Chalupa LM (eds) The new visual neurosciences. MIT Press, Cambridge, pp 1153–1163

Wheeler WM (1928) The social insects. Their origin and evolution. Kegan Paul, Trench and Trubner; Harcourt and Brace, London; New York

Wittlinger M, Wehner R, Wolf H (2006) The ant odometer: stepping on stilts and stumps. Science 312:1965–1967

Wolf E (1927) Über das Heimfindevermögen der Bienen. II. Z Vergl Physiol 6:221–254

Wystrach A, Beugnon G, Cheng K (2011) Landmarks or panoramas: what do navigating ants attend to for guidance? Front Zool 8:21. doi:10.1186/1742-9994-8-21

Wystrach A, Mangan M, Philippides A, Graham P (2013) Snapshots in ants? New interpretations of paradigmatic experiments. J Exp Biol 216:1766–1770

Zeil J, Hofmann MI, Chahl JS (2003) Catchment areas of panoramic snapshots in outdoor scenes. J Opt Soc Am A 20:450–469

Ziegler HE (1920) Der Begriff des Instinktes einst und jetzt. Eine Studie über die Geschichte und die Grundlagen der Tierpsychologie. Mit einem Anhang: Die Gehirne der Bienen und Ameisen. 3rd revised and extended edn. G. Fischer, Jena