

After that, they were coasting, or even slowing down, in terms of the turnover of species origins and extinctions.

There was a long-held assumption that dinosaurs rose to prominence through a process of large-scale competition, in which they actively expanded their ecospace at the expense of other Triassic tetrapods, such as the synapsids (mammal-like reptiles including dicynodonts) and crurotarsan archosaurs. In a macroevolutionary exploration of dinosaurian origins, Steve Brusatte and colleagues found that dinosaurs expanded in diversity and disparity through the Late Triassic. However, the diversity and disparity of their supposedly inferior competitors, the crurotarsans, were increasing at about the same rate. After the Crurotarsan largely died out during the mass extinction at the end of the Triassic, the dinosaurs diversified a little, but did not expand their morphospace substantially.

The conclusion that dinosaurs emerged without making a major impact on their supposed competitors was confirmed in a phylogenetic comparative study by Roland Sookias and colleagues, who explored changing body size through time. In a phylogenetic context, the shrinking mean size of the synapsids and the increasing mean size of the archosaurs and relatives both followed Brownian-Motion models. This means the rates of change cannot be distinguished from random walks, and hence evolution is described as 'passive' rather than 'active'. Dinosaurs likely originated opportunistically, following extinction events, rather than by active replacement of competitors.

### Conclusion

Of all the geological periods, the Triassic stands out as unusual in that it serves to document recovery from the largest of all mass extinctions. This massive punctuation in the history of life marked the origin of modern ecosystems. Documentation of the fossil record of the Triassic has improved tremendously thanks to astonishing new discoveries from China. Further, the accuracy and precision of dating and correlation worldwide have improved enormously. Geologists are also able to reconstruct ancient continental distributions, climates, and atmosphere-ocean biogeochemical cycles with confidence.

Future work will concentrate on filling gaps and extending fossil ranges. Methods of discovering and dating phylogenetic trees will continue to improve, and computational methods of exploring these patterns to derive models in macroevolution mark a rich opportunity for new research.

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# Unsupervised statistical learning in newly hatched chicks

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The ability to extract probabilistic information from visual inputs has been reported in human adults and infants (reviewed in [1,2]), and in adults of non-human species, though only under supervised (conditioning) procedures [3]. Here, we report spontaneous sensitivity to the probabilistic structure underlying sequences of visual stimuli in newly hatched domestic chicks using filial imprinting, suggesting that statistical learning may be fully operating at the onset of life in precocial avian species.

We exposed visually naive, newly hatched chicks to a stream of four shapes for 2 hours. Shapes were presented one at a time in the centre of a computer screen. The order was defined by transitional probabilities (TPs) within/between shape-pairs. Each shape was presented for two seconds and loomed from 2 to 10 cm in height in a continuous loop (see Supplemental Information for details). The familiar sequence consisted of two shape-pairs defined by statistical dependencies within and between pairs' elements. For instance (Figure 1A left), Pair 1 consisted of a *square* always followed by an *X-shape* (TP within-pair = 1.0) and Pair 2 consisted of a *circle* always followed by a *triangle* (TP within-pair = 1.0). Because there were no pauses between pairs, the only cue available to segment the stream was the statistical structure of the sequence (TP between pairs = 0.5).

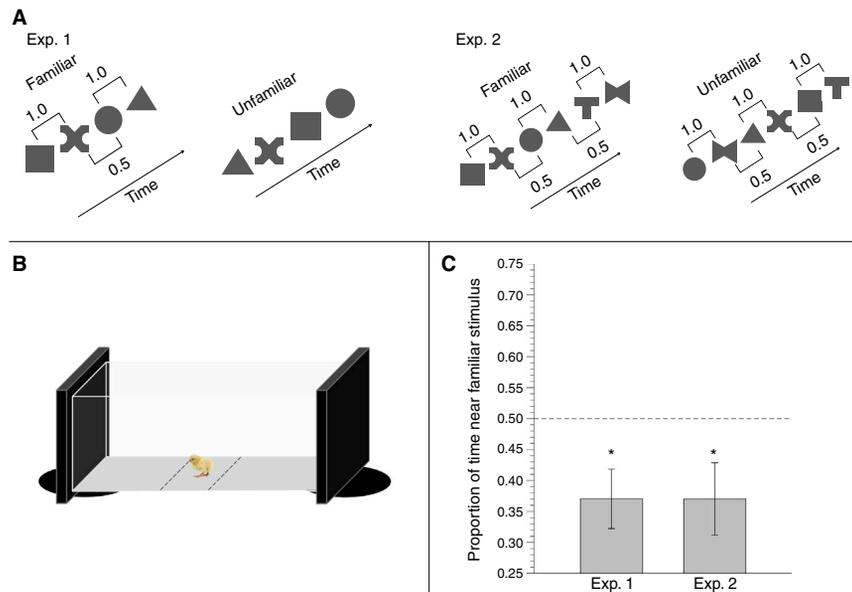
The apparatus consisted of two identical computer screens placed at the opposite ends of a runway, simultaneously playing the two test sequences (Figure 1B; see Supplemental Information for details). The chicks' behaviour was recorded for six consecutive minutes by a camera placed above the apparatus.

In Experiment 1, the test stimuli consisted of the familiar stream and an unfamiliar stream: a semi-random

generation of the same four items (see Supplemental Information). The semi-random ordering was not constrained by any statistical relations within or between shapes, but two identical shapes never appeared consecutively (Figure 1A, left).

A significantly higher number of chicks approached the unfamiliar stimulus first (46 chicks out of 74,  $\chi^2 = 4.37$ ,  $p = 0.036$ ). Consistent with this finding, a significantly higher proportion of time was spent by chicks near the screen playing the unfamiliar sequence ( $t_{(73)} = -2.69$ , mean = 0.37,  $p = 0.009$ , s.e.m. = 0.04, Cohen's  $d = -0.317$ , 95% CI = [-0.22, -0.03]; Figure 1C). Chicks were clearly able to distinguish the familiar (statistically defined) sequence from the unfamiliar (random) presentation of the same items. They expressed their choice as a novelty preference rather than approaching the familiar stimulus; this was expected because choice for slight novelty has been typically reported in chicks under relatively short exposure of a stimulus (the imprinting object) when test stimuli resemble it (reviewed in [4]). In a natural environment this is likely to favour imprinting on siblings, who are slightly different from each other.

In Experiment 2 (Figure 1A, right), another pair of shapes was added to the exposure sequence (as well as to test stimuli) in order to make the task more demanding. Moreover, the unfamiliar test sequence was this time a novel, structured combination of the familiar shapes rather than a random combination of the familiar shapes, as in Experiment 1. The familiar statistical relations among shapes were thus reset at test by re-organizing the same elements into new pairs that the animals had never experienced before. For instance, in the familiar sequence, the *circle* always predicted the *triangle* whereas in the unfamiliar sequence the *circle* always predicted the *butterfly*. This change made Experiment 2 more challenging than Experiment 1, in which chicks merely had to discriminate the familiar structure from a stimulus that did not possess any statistical regularity. As the new unfamiliar sequence was also statistically constrained, chicks were required to discriminate two structured sequences of objects. We also included another change to test sequences which were perceptually segmented



**Figure 1. Illustration of stimuli and apparatus used in Experiments 1 and 2.**

(A) Left: test-version of the familiar sequence and representation of the unfamiliar random stimulus used in Experiment 1. Right: test-version of the familiar sequence and test-version of the unfamiliar structured sequence used in Experiment 2. (B) Representation of runway and computer screens used during testing. (C) Proportion of time spent by each chick near the screen presenting the familiar stimulus, for both Experiment 1 and Experiment 2. Error bars show standard errors of the means. Asterisks indicate significant departures from chance level (0.5, marked by the dotted line).

by a two-second visual break inserted between each pair (see Supplemental Information).

The results (Figure 1C) show that a significantly higher number of chicks first approached the unfamiliar rather than the familiar stimulus (32 chicks out of 48,  $\chi^2 = 5.33$ ,  $p = 0.021$ ) and a significantly higher proportion of time was spent by chicks near the screen presenting the unfamiliar rather than the familiar sequence ( $t_{(47)} = -2.21$ , mean = 0.37,  $p = 0.032$ , s.e.m. = 0.05, Cohen's  $d = -0.325$ , 95% CI = [-0.24, -0.01]).

We thus demonstrated a spontaneous sensitivity to the probabilistic structure of a sequence of visual stimuli in naïve, newly hatched chicks. The sequence was presented as a continuous stream of individual elements the ordering of which was defined by transitional probabilities within/between shape-pairs. After exposure to a structured sequence in the absence of reward, chicks were capable of discriminating this pattern from a random generation of the same elements (Experiment 1) and from a novel, statistically constrained combination of the elements (Experiment 2).

The ability to track statistical regularities from visual inputs seems to

be still quite immature in one- to three-day-old human neonates, who showed no evidence of learning when more than four items composed the sequences [5]. In contrast, chicks successfully tracked the statistical structure of both four- and six-element sequences, suggesting that visual statistical learning is entirely effective at the onset of life in this precocial species.

In our experiments, chicks were merely exposed to the statistically defined stimulus before being tested. The learning process, possibly mediated by filial imprinting, was thus “unsupervised” [6] as the chicks extracted the structure of the sequence without relying on any external feedback or reinforcement. This capacity for unsupervised statistical learning adds to evidence for unsupervised rule learning [7,8] and, broadly, for pattern generalization [9] in precocial species.

In a natural environment, newly hatched chicks must recognize their mother hen and siblings independent of the visual perspective and, given that different views of social partners likely follow one another over short periods of time, it has been suggested that chicks lump together all these views to build

up a representation of the whole social companion [10]. A sensitivity to ordered transitional probabilities of different images that are rapidly alternated might thus lie at the foundation of such ability.

#### SUPPLEMENTAL INFORMATION

Supplemental Information including experimental procedures can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2016.10.011>.

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# *Plasmodium falciparum* malaria in 1<sup>st</sup>–2<sup>nd</sup> century CE southern Italy

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The historical record attests to the devastation malaria exacted on ancient civilizations, particularly the Roman Empire [1]. However, evidence for the presence of malaria during the Imperial period in Italy (1<sup>st</sup>–5<sup>th</sup> century CE) is based on indirect sources, such as historical, epigraphic, or skeletal evidence. Although these sources are crucial for revealing the context of this disease, they cannot establish the causative species of *Plasmodium*. Importantly, definitive evidence for the presence of malaria is now possible through the implementation of ancient DNA technology. As malaria is presumed to have been at its zenith during the Imperial period [1], we selected first or second molar from 58 adults from three cemeteries from this time: Isola Sacra (associated with Portus Romae, 1<sup>st</sup>–3<sup>rd</sup> century CE), Velia (1<sup>st</sup>–2<sup>nd</sup> century CE), and Vagnari (1<sup>st</sup>–4<sup>th</sup> century CE). We performed hybridization capture using baits designed from the mitochondrial (mtDNA) genomes of *Plasmodium* spp. on a prioritized subset of 11 adults (informed by metagenomic sequencing). The mtDNA sequences generated provided compelling phylogenetic evidence for the presence of *P. falciparum* in two individuals. This is the first genomic data directly implicating *P. falciparum* in Imperial period southern Italy in adults.

The story of malaria in Imperial Italy is drawn from a rich historical narrative; see, for example, Hippocrates' *On Epidemics*, Celsus' *De Medicina*, or Galen's *De Morborum Temporibus*. These texts describe the classic fever periodicity — tertian, semi-tertian, quartan or quotidian — that have been

documented since the 5<sup>th</sup> century BCE. Despite this, the timing and geographical range of malaria remains uncertain, as only a broad northward spread is thought to have occurred across Italy from 500 BCE to 1000 CE [2]. The inability to connect malaria to a precise historical and geographical space in antiquity is further complicated by its pathogenesis, as this infection does not cause distinct pathological changes to the human skeleton, although non-specific skeletal indicators of physiological stress are prevalent in malarious environments [3]. Furthermore, the existing molecular evidence for malaria in Imperial Italy currently consists of a single PCR product corresponding to *P. falciparum* from an infant from 5<sup>th</sup> century CE Lugnano in Umbria [4]. The prevalence and influence of malaria among adults in southern Italy therefore remain unknown.

Malaria is responsive to climate, topography, human activity, and ecology on a local scale, so there is likely no single mortality profile that is applicable to all of Imperial-period Italy [1,2]. Accordingly, we used ecologically diverse coastal and rural localities to determine the presence of *Plasmodium* through ancient DNA technology. We focused on Velia (a coastal promontory between alluvial plains) [5], Portus Romae (a low-lying basin of woodlands near the Tiber River alongside marshes and lagoons) [6], and inland Vagnari (a wooded river valley with lowland hills) [7] (Figure S1A).

We detected *P. falciparum* mtDNA fragments from two individuals, LV13 (Velia) and LG20 (Vagnari), dating to the 1<sup>st</sup>–2<sup>nd</sup> century CE (Figure 1A), with no positive results from the Portus Romae samples, although this does not preclude the presence of malaria in this locality (Table S1). Through an RNA-bait set designed from four human and two non-human *Plasmodium* species, we were able to enrich a total of 3,033 bp (120 reads total), or 50.8% of the 5,967 bp *P. falciparum* mitochondrial genome, when reads from LG20 and LV13 were combined. Separately, LG20 yielded 300 bp (7 reads) and LV13 yielded 2,901 bp (113 reads). Although our baits will enrich for *P. vivax* and *P. malariae*, which may have co-circulated with *P. falciparum*, we did not detect any reads matching these species. Importantly, *Plasmodium*