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Biogeography of the Indonesian coelacanths

Living coelacanths (Latimeria chalumnae) are normally found only in the western Indian Ocean, where they inhabit submarine caves in the Comores Islands¹. Two specimens have since been caught off the island of Manado Tua, north Sulawesi, Indonesia, some 10,000 kilometres away². We sought to determine the ecological and geographic distribution of Indonesian coelacanth populations with a view to drawing up conservation measures for this extremely rare fish^{2,3}. During our explorations, we discovered two living Indonesian coelacanths 360 km southwest of Manado Tua.

Analysis of mitochondrial DNA from a single Indonesian specimen, described as a distinct species, L. menadoensis⁴, revealed significant differences with the published mitochondrial genome of L. chalumnae. These differences indicate that the Indonesian and Comoran coelacanths diverged 1.8–11.0 million years ago⁵.

In an attempt to find more fish, we performed a total of 34 dives in the research submersible IAGO down to a depth of 400 metres at points along the northern coast of Sulawesi, the Sangihe islands and the Bay of Tomini in central Sulawesi. We failed to find any coelacanths during seven dives off Manado Tua, where the two previously reported coelacanths were caught², but 360 km southwest of Manado Tua we found two coelacanths approximately 120 and 140 cm long in a deep carbonate cave at a depth of 155 m (water temperature, 17.8–20.1 °C).

The substrate and oceanographic conditions in the Indonesian and Comoran dive sites are completely different. The Comores have steep, young volcanic slopes with numerous lava caves, whereas the slopes of the Indonesian dive sites are older, more eroded and less steep, with very few caves, and these are mainly carbonate in origin. The Indonesian sites are exposed to strong currents (with an estimated peak velocity of 3-4 knots) of variable directions and with sudden up- and downwellings. In contrast, the Comoran habitat is frequently devoid of currents, and these are slower than 1 knot.

These differences may be important, as

Comoran coelacanths are sluggish, nocturnal drift hunters that feed on other fish and have a low metabolic rate⁶. During the day, they retreat to the still water of deep lava caves¹. The Indonesian sites would therefore seem to be unsuitable for sustaining a viable population of *L. chalumnae*.

So far, four Indonesian coelacanths have been found in a relatively small area along the north Sulawesi coast. We suggest that the population is very small and requires strict conservation measures. But we cannot exclude the possibility that the coelacanths of north Sulawesi are derived from a different area and drifted there with oceanic currents. The dominant current driving Indonesian throughflow water in the area of north Sulawesi is the southerly Mindanao current⁷, indicating that the potential source population may be in the southern Philippines or remote Pacific islands.

Furthermore, geological evidence and our genetic studies of the Comoran population indicate a young age for this population of less than 100,000 years. The reported older genetic separation of the Indonesian coelacanth of more than 1 million years would suggest that Comoran L. chalumnae probably derived from a third, as yet unknown, population.

The biogeography of the new coelacanth population remains enigmatic, although perhaps this is for the best. An undiscovered home is probably the best possible protection for these endangered fish.

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Extrapolating movement without retinal motion

In contrast to the perception of a stationary object that is briefly flashed in the dark, a continuously visible moving object is seen as being ahead of its actual position at the time of the flash. An explanation for this simple effect, in which a stimulus moving on the retina is seen as being further along its path and not where it was in space when its signal impinged on the retina, is keenly debated¹⁻⁶. We show here that this illusion is not just limited to retinal motion, and that perceptual mislocalization occurs even when stimulus motion is inferred entirely from extra-retinal information, for example by movement of the observer's head or whole body, without retinal motion. The phenomenon may therefore rely on a much more general mechanism.

Nijhawan^{1,2} originally suggested that the illusion is the product of a brain process that tries to overcome at least some of the visual transmission delay (more than 50 ms) through extrapolation, so that we should be able, for instance, to catch a moving object accurately. Other observations3,4 indicated that the apparent stimulus misalignment could be the passive consequence of the difference in the afferent delay between a stimulus that is moving on the retina and a stationary one. The physiological properties of the retina itself may even be sufficient to produce the misalignment⁶. These explanations are all based on retinal motion, however, which is the only condition under which the phenomenon has so far been demonstrated.

We set up two situations in which the movement of the stimulus in space was generated entirely by the movement of the

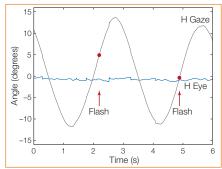


Figure 1 Recording of horizontal eye movement relative to external space, and eye movement relative to the head. The subject rotated his head sinusoidally back and forth while fixating a light-emitting diode array mounted on a recording Eyelink helmet. Flashes occurred at times indicated by arrows and were perceived as lagging behind the continuously lit stimulus. Subjects estimated the perceptual misalignment in this condition by comparing it afterwards, head fixed, with the misalignment of the same stimulus rotating on a turntable at 30 revolutions per minute, as previously1,2,

observers, without retinal motion. In the first situation, five subjects (two authors and three naive subjects) wearing the helmet of an eye-tracking system (Senso-Motoric Eyelink) focused their gaze on a vertical bar made up of light-emitting diodes (LEDs). The bar was mounted on the helmet 36 cm in front of the eyes. In complete darkness, subjects were instructed to rotate their heads horizontally back and forth (at 20-30 degrees, with a rhythm of about 0.3-0.4 Hz). The lower two-thirds of the bar (26 mm × 1.5 mm) was continuously lit, while the upper one-third of the bar was flashed for 6 ms halfway through the head movements.

The recordings showed that, while gaze (the position of the eye in space) moved approximately 25 degrees per cycle (Fig. 1), the total eye displacements relative to the head were less than 1 degree per cycle. Furthermore, no eye displacement in the head occurred at the time of the flashes, so the motion of the stimulus on the retina was minimal compared with the motion of the stimulus in space.

When the subjects were asked to judge the position of the array with respect to the position of the flashed LEDs, however, they invariably reported that the continuously lit LEDs were ahead of the flashed ones. Even though all subjects, including the naive ones, had seen the LED array before the experiment and knew that all the LEDs were fixed on a single rigid bar, they still perceived a misalignment of several degrees of visual angle between the continuously lit and the flashing segments, as in earlier studies in which there was retinal motion^{1,2}. When the subjects were continuously rotated in a chair at 20 revolutions per minute, the visual stimulus was the same. The continuously lit moving stimulus was seen as leading, most clearly at the start of rotation, and as lagging during the final deceleration.

The brain has no direct access to the timing of external events because input delays are variable and therefore unreliable³. When moving stimuli are involved, uncertainty about the time of an event (for example, of a flash) can translate into uncertainty about position. The time-position ambiguity resulting from processing delays may affect the perception of stimulus motion, regardless of how the brain has access to this information. Whether the cue derives from retinal, oculomotor, vestibular or proprioceptive signals, the perceived position of a moving object may be extrapolated in the same way.

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Numerical memory span in a chimpanzee

A female chimpanzee called Ai has learned to use Arabic numerals to represent numbers¹. She can count from zero to nine items, which she demonstrates by touching the appropriate number on a touch-sensitive monitor^{2,3}, and she can order the numbers from zero to nine in sequence⁴⁻⁶. Here we investigate Ai's memory span by testing her skill in these numerical tasks, and find that she can remember the correct sequence of any five numbers selected from the range zero to nine.

Humans can easily memorize strings of codes such as phone numbers and postcodes if they consist of up to seven items, but above this number they find it much harder. This 'magic number 7' effect, as it is known in human information processing⁷, represents a limit for the number of items that can be handled simultaneously by the brain.

To determine the equivalent 'magic number' in a chimpanzee, we presented our subject with a set of numbers on a screen, say 1, 3, 4, 6 and 9. She had already displayed close to perfect accuracy when required to choose numerals in ascending order, but for this experiment all the remaining numbers were masked by white squares once she had selected the first number. This meant that, in order to be correct in a trial, she had to memorize all the numbers, as well as their respective positions, before making the first response. Chance levels with three, four and five items were 50, 13 and 6%, respectively.

Ai scored more than 90% with four items and about 65% with five items, significantly above chance in each case. In normal background trials, response latency was longest for the first numeral and much

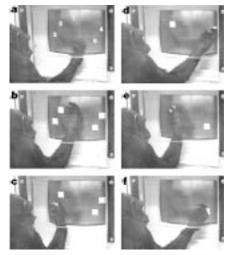


Figure 1 The chimpanzee Ai performing the five-number ordering task in the 'masking' trial. Five numbers (1, 3, 4, 6 and 9) are presented on the touch-sensitive monitor. a, b, Ai correctly chooses the number 1 as the lowest of the series (a), at which point the remaining numbers are automatically masked (b). c-f, She continues to identity the numbers one by one in ascending order (c-e), ending with the 9 (f). See Supplementary Information and http://www.pri.kyoto-u.ac.jp for more details.

shorter for all the others, indicating that Ai inspected the numbers and their locations and planned her actions before making her first choice. In masking trials, response latency increased only for the choice directly after the onset of masking, but this latency was similar to those recorded in background trials, indicating that successful performance did not depend on spending more time memorizing the numbers.

In one testing session, after Ai had chosen the correct number and all the remaining items were masked by white squares, a fight broke out among a group of chimpanzees outside the room, accompanied by loud screaming. Ai abandoned her task and paid attention to the fight for about 20 seconds, after which she returned to the screen and completed the trial without error.

Ai's performance shows that chimpanzees can remember the sequence of at least five numbers, the same as (or even more than) preschool children. Our study and others $^{8-10}$ demonstrate the rudimentary form of numerical competence in nonhuman primates.

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Table	1	Performance	in	masking	trials		

	Number (% correct)						Response time (ms)						
Type of trial	Numbers	Trials	1st	2nd	3rd	4th	5th	Total	1st	2nd	3rd	4th	5th
Normal	2	405	98	100	_	_	_	98	676	420	_	_	_
Normal	3	433	97	97	100	_	_	94	710	424	420	_	_
Normal	4	451	93	96	98	100	_	87	754	439	407	412	_
Normal	5	421	90	93	94	99	100	78	799	448	415	430	408
Masking	3	200	98	91	100	_	_	89	768	533	465	_	_
Masking	4	20	100	100	95	100	_	95	717	390	432	437	_
Masking	5	20	95	95	89	81	100	65	721	446	426	466	411

1st, 2nd, 3rd, 4th and 5th refer to the numbers in a sequence in ascending order.