Cambridge University, NST Psychology Part II, Section B, Comparative Cognition

a. Absolute brain size
b. Relative brain size.
c. Encephalisation Index: relates a species’ actual brain size ($E_a$) to the expected brain size ($E_e$). $k = E_a / E_e$
d. Cerebral cortex: look at the size of cortical areas as these are the areas that are most likely to be involved in cognitive processing.
e. Neocortex
f. Prefrontal cortex, which is involved in planning and reasoning.
g. Cortex organisation, e.g. number of neurons, conduction velocity.
h. Adaptations of the brain: the more important a function for a species, the more brain will be devoted to it as a proportion of total brain volume.
i. Behavioural indicators of intelligence: how the animal's behaviour is measured and which cognitive mechanism underlies the behaviour are both factors that need to be considered. Tests of behaviour, e.g. learning sets.
j. Adaptive specialisations of behaviour, e.g. food-storing birds perform better on spatial memory tasks than other birds, but not on visual memory tasks.

5. Selection pressures shaping intelligence:
   a. The foraging theory of intelligence.
   b. The social theory of intelligence, including the Relationship Quality Hypothesis.
   c. Sexual selection of intelligence.

What is intelligence?

Humans seem to have an implicit understanding of intelligence and intuitively assume that different species can be ranked according to their intelligence. It has been suggested that people rank the intelligence of animals based on the degree of physical similarity to humans and the extent to which they formed an attachment with that particular species ('pet owner phenomena').

However, cognitive abilities of animals are not ordered in a linear progression, but rather in terms of a phylogenetic tree. Due to divergent evolution closely related species become more dissimilar. However, distantly related species that face similar socio-ecological problems in their environment may possess the same cognitive abilities (convergent evolution).

A very generalist view of intelligence is that it consists of domain-general processes, which might be common to all animals.

Another view is to consider both domain general and specific processes. Species differ because they have adapted to different environments that have different sets of problems to solve. Thus many believe that mental or behavioural flexibility might be a good way of defining intelligence. Behavioural flexibility means that animals are able to produce novel solutions to problems that are not part of the animal's normal repertoire. This could be tested in the lab by presenting animals with problems that they do not encounter in the wild or by observing innovations in the wild.

How can intelligence be measured?

1. The brain as an indicator of intelligence:
The Relationship Quality Hypothesis was formulated in relation to birds. For life-long socially monogamous birds, intelligence might have been shaped by the demands of living in a pair-bond and be closely related to cooperative behaviours important for establishing and maintaining long-term relationships. Thus, it might be the quality rather than or in addition to the quantity of interactions, that underlies these birds' intelligence.

3. Sexual selection of intelligence: humans are thought to have evolved large brains because the associated cognitive abilities were effective in attracting mates and thus led to enhanced reproductive success. Experimental evidence shows that humans are attracted to those who are intelligent.

An example of how choosing a mate with higher cognitive abilities might directly enhance the chooser’s fitness is the case of pinyon jay females, who are dependent on their mates for food from cache recovery during incubation, breeding and feeding the offspring. Thus the male’s spatial cognitive abilities are hypothesised to have a strong impact on both the male’s and the female’s reproductive success. However, it yet remains to be tested whether females choose their mates according to their spatial cognitive abilities.

Lecture 5 - Spatial Learning and Cognitive Maps

Summary

1. Trail following
2. **Dead reckoning** (navigating from a known location using internal cues of direction and distance), allowing **path integration** (taking a direct route). E.g. bees use optic flow, and ants use the number of steps taken.
3. Compass use. E.g. pigeons use a sun compass, and bees use the azimuth of the sun in their dances.
4. Odour mapping: gradients could also be extrapolated beyond the range of immediate experience, such that animals could be able to get home from unfamiliar sites. E.g. pigeons.
5. Landmark use: e.g. digger wasps, bees, Eurasian jays. Preference has been shown for large, 3D landmarks. Wasps and bees seem to follow the **retinal snapshot hypothesis**, whereby landmarks are remembered by storing the retinal image at the goal location (uses the array of landmarks). Gerbils treat every landmark individually and seem to learn the distance and direction of each landmark from the goal.
6. Geometrical relations: animals are sensitive to the geometric shape made by a series of landmarks. E.g. rats, toddlers and digger wasps.
7. **O'Keefe and Nadel** defined a cognitive map as a unitary, allocentric, connected spatial representation, in which experiences locate objects and events. Classical ways to experimentally test whether an animal possesses a cognitive map are tests of whether animals are able to take shortcuts to a goal in a familiar environment, whether animals can choose a correct detour when their usual route is blocked, and whether animals can ‘knit together’ information acquired on different journeys into a single allocentric representation. Bees may use cognitive maps: older foragers can fly directly home if captured whilst leaving their hive, and transported to a different location in darkness and after seeing experienced foragers dance indicating (experimentally manipulated) food locations either on the far shore of a lake or in the middle of the lake, recruiters fly off in the direction of the former but not the latter. Gould’s original experiments suggested that bees use cognitive maps, but
which represents the angle between the sun’s azimuth and the food source. On overcast days they use their memory to predict the sun’s azimuth.

4. **Odour mapping**: gradients could also be extrapolated beyond the range of immediate experience, such that animals would be able to get home from unfamiliar sites. Examples:
   a. Pigeons: there is poor homing performance in pigeons that are deprived of olfactory perception. Unusual wind direction also produces poor homing performance due to vanishing odours. Pigeons that are allowed to smell the air at their release site show faster homing speeds. Pigeons only use odour at large distances from home - suggesting that they rely on landmarks in known areas.

5. **Landmark use**: e.g. digger wasps, bees, Eurasian jays. Preference has been shown for large, 3D landmarks. One theory of landmark use is the **retinal snapshot hypothesis**. This proposes that landmarks are remembered by storing the retinal image at the goal location. Wasps and bees perform orientation flights after their first departure from the nest to form these retinal snapshots. When a single, symmetrical landmark is used, animals still know exactly where the goal is, suggesting they may use some other cues to guide them as well. Examples:
   a. Bees: navigate using the retinal snapshot hypothesis. When trained with a single cylindrical landmark and tested with landmarks of different sizes, bees learnt the apparent size and bearing of the landmark as seen from the food source and in the test fly to a position where the retinal image matched the remembered image. Thus, when the landmark was doubled in size, the bees searched twice as far way and when the landmark was halved, the bees searched twice as close.
   b. Gerbils: treat every landmark individually and do not only rely on a global property of the array. They seem to learn the distance and direction of each landmark from the goal. For example, if a gerbil is trained a red food south in the mid-point of two landmarks and when tested with only one landmark, the gerbils searched at the correct distance either south-east or south-west of the landmark. When tested with the two landmarks placed further apart, gerbils searched in two discrete areas.

6. **Geometrical relations**: animals are sensitive to the geometric shape made by a series of landmarks. Digger wasps disregarded landmarks consisting of the same pinecones as the original one if it changed its shape but used landmarks of the same shape made out of stones. Rats tend to ignore landmarks (unless in a familiar environment or highly motivated) but use geometry, as do toddlers (it is not until the age of six that children begin to use landmarks as well).

Do animals use cognitive maps to navigate?

Tolman said that a cognitive map allows an animal to make short cuts between two points. This refers to the animal being able to take a shortcut to a goal. O'Keefe and Nadel expanded the idea by defining a cognitive map as a unitary, allocentric, connected spatial representation, in which experiences locate objects and events.

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congregate in large colonies, where juveniles associate with many non-relatives as well as kin, and parrots are also renowned for their sociality.

4. Like apes, corvids and parrots are also omnivorous generalists and show a great propensity to find innovative solutions to novel problems, from the manufacture of tools to the protection of food from competitors. For example, keas readily raid rubbish bins for food and appear to take great delight in destroying cars. Japanese crows in Sendai City have learned to crack nuts safely by dropping them onto pedestrian crossings and waiting until the traffic lights turn red before retrieving the nut's contents. Rooks at a motorway service station in England have discovered a novel method for gaining access to food thrown in rubbish bins. They cooperate in pulling up the bin liner and then either feed from the raised food or toss the contents onto the ground where the waiting crowds of colony mates reap the rewards.

5. The propensity to show innovative foraging solutions correlates with brain size. Within the birds, corvids have the largest brains and highest rates of innovation; and within mammals, apes have the highest rates. Indeed, the relative forebrain size of corvids and parrots is as large as that of the non-human apes, and considerably larger than that of rats and pigeons.

6. Detailed observations of captive colonies of rooks suggest they form complex social networks, in much the same way as chimpanzees do.

7. Convergent evolution of tool use in apes and corvids:

The New Caledonian crow is extraordinarily skilled at making and using tools. The only other animals to display this diversity and flexibility in tool use and manufacture are the great apes. Chimpanzees have been observed to manufacture a range of different tools that are used for specific purposes, and different geographic populations of chimpanzees use different tools for different uses, suggesting that there may be cultural variations in tool use. Observations of the crows' tool use in the wild also suggest similar levels of cultural complexity. For example, there is potential cumulative evolution in the complexity of stepped tools, and crows from different geographical areas have different designs of tool.

8. Emery and Clayton (2004) suggest that apes and corvids use four cognitive tools to overcome similar environmental problems:

a. **Causal reasoning**: tool use and manipulation suggest that some corvids, like apes, may understand the causal relationships by which these tools operate or are effective (however, the role of basic instrumental conditioning remains unclear). Weir et al, 2002, showed that Betty the corvid could innovatively manufacture tools in the lab. Furthermore the recent work on physical cognition by rooks suggests that at least one bird has a basic understanding of some aspects of folk physics.

b. **Flexibility**: apes and corvids show flexible behaviour, in that they can generalise learned rules in order to apply them to novel stimuli or situations. When presented with a series of different discriminations to learn, corvids, like apes, extract the general rule such as win-stay, lose-shift rather than having to learn each new discrimination afresh. By contrast, pigeons appeared to be rote learners, solving the task eventually by learning each discrimination individually. Corvids also demonstrate superior abilities in other transfer problems such as transitive inference tests (A>B>C>D), in which the birds are trained on an ordered set of various pair-wise comparisons (e.g. A+ B-, B+ C-, etc.). On test, they must transfer information about the dyadic relationships to novel pairs (e.g. B vs. D) to solve the
the call simply trigger a particular behavioural response (‘look up at the sky and make a dash for
cover’ versus ‘run up the tree if you are on the ground, but stay up in the tree if you are already
there’)? Zuberbühler and colleagues (1999) used the habituation transfer design of Seyfarth &
Cheney (1980) in which the animals were exposed to a ‘prime’ stimulus to which they habituated
followed by a second ‘probe’ stimulus. There were three types of condition: (a) baseline in which
the two calls were similar in both acoustic and semantic features; (b) test in which the two calls were
acoustically different but similar in semantic features; or (c) control in which the two calls differed in
both acoustic and semantic features. It is the test condition that is critical. If the monkeys only
attended to the acoustic features of the call regardless of meaning then they should show a strong
response to the eagle call on test, because the acoustic structure of the monkey’s eagle alarm call is
very different to that of the eagle’s call. By contrast, if the monkeys understand that the eagle alarm
call means ‘eagle’ then they should produce a low response to the eagle call in the test condition.
This is precisely what the monkeys did. Now, although these results suggest that natural primate
communication may possess semantic properties, evidence for syntactical rules is lacking.

Primate Language Training: Comparative Psychologists have been to great lengths in their attempts
to teach chimpanzees to speak, but such attempts were doomed to failure. Like other non-human
primates, chimpanzees do not have the appropriate vocal tract to form the speech sounds used in
human language (Fitch, 2000).

Sign language: Later studies therefore focused on training chimpanzees to learn American Sign
Language (ASL), capitalising on the fact that apes use hand gestures in their natural communication.
Washoe, a chimpanzee, was taught 132 signs (Gardener & Gardener, 1969). Similar abilities have
been reported for Chantek, an orangutan (Miles, 1990) or Koko, a gorilla (Patterson & Linden,
1981). It was claimed that these apes could combine signs into strings of signs according to
syntactical rules and that they could make new combinations such as Washoe signing ‘water bird’ to
represent a swan. However, evidence is that Washoe intended these two signs to refer to one
thing, i.e. a sign to signing for ‘water’ and ‘bird’?

Indeed, a more careful study of the acquisition of ASL by an infant chimpanzee, Nim Chimpsky,
raised questions about what the chimpanzees understood when using these signs or gestures
(Terrace et al, 1979). Nim acquired a vocabulary of about 125 words over a period of three and a half
years. A 2-year old child acquires a vocabulary of about 10 words a day, so Nim’s 125 word
vocabulary would have been less than a fortnight’s work for a typical human toddler! Nim was not
able to produce long strings of signs, and showed no evidence of understanding syntactical structure
in the way that young children rapidly learn to do. Furthermore, careful analysis of the videos
recorded during signing sessions for both Nim and Washoe suggested that many of the strings of
signs produced were just imitations of the trainer’s signing as opposed to spontaneous formation of
signs in response to questions.

Token language: Premack (1971) trained Sarah, a language-trained chimpanzee, to use plastic
tokens to represent objects. Premack claimed that she could then use the tokens to understand
word strings that had particular meanings, even when they were novel. Another chimpanzee, Lana,
learned that visual icons on a keyboard (a ‘lexigram’) represented different words (‘Yerdish’)
(Rumbaugh, 1977). Two other chimpanzees in Rumbaugh and Savage-Rumbaugh’s laboratory,