Zuerst ersch. in : The Oxford handbook of comparative cognition / Thomas R. Zentall, Edward A. Wassermann [eds.]. - Oxford [u.a.] : Oxford Univ. Press, 2012. - S. 693-717. - ISBN 978-0-19-539266-1

Intelligences and Brains

An Evolutionary Bird's-Eye View

Juan D. Delius *and* Julia A. M. Delius

Abstract

This chapter is an interdisciplinary consensual overview of intelligence as a behavioral disposition displayed by some animals, including humans. Topics discussed include animal intelligence, human intelligence, intelligence varieties and brain correlates; concept formation, transitive responding, and mental rotation; intelligence development and intelligence evolution.

Keywords: animal intelligence, human intelligence, intelligence testing, concept formation, transitive responding, mental rotation, brain size, intelligence development, intelligence evolution

Whenever reporting on the cognitive abilities of animals to lay audiences, one is regularly confronted with the question of whether one is suggesting that animals are, in fact, intelligent. The senior author has often found himself sidestepping this question, but having taken over a seminar on intelligence in animals, humans, and machines, he could no longer evade it. Moreover, the participants complained that the seminar's readings conveyed a mere mass of disconnected knowledge; they wanted a succinct text that would organize the material. This chapter is an updated version of that text, which presents what the authors consider to be an interdisciplinary consensual overview of intelligence as a behavioral disposition displayed by some animals, humans included.

There has never been any doubt about the fact that the human species is the cleverest on Earth. However, there has been much preoccupation with the circumstance that not all human individuals are equally bright. In nearly all areas of human endeavor, it is appreciated that the degree of cleverness or stupidity of an individual is a factor that defines the efficiency with which he or she can execute all but the most routine tasks. This efficiency is mostly judged by the accuracy, the speed, and the effortlessness with which a person can solve everyday problems. These problems might involve finding the way in unknown terrain with a map, baking a cake when ingredients and implements are lacking, assembling kit furniture without the instructions, or setting straight a muddled scientific text. Although there is no undisputed definition of intelligence, there is some consensus that it has to do with varying abilities to quickly and successfully adapt behavior to novel situations, or more abstractly, with varying capacities for a (rapid) goal-conducive processing of cognitive information (Hunt, 1980).

A test that measured intelligence was first devised by Alfred Binet (1857–1911). Intelligence tests were steadily improved so that now several of them provide a consistent, replicable, and predictive measure of individual intellectual ability (Kaufman, 2000). Early tests tended to yield scores that were much influenced by the cultural background and the formal education that the subjects had experienced. Modern intelligence tests are designed to be largely insensitive to these factors. An extreme in this respect are the so-called Raven scales, which are thought to give nearly ideal measures of the general intelligence of individuals independently of their particular expertises and also independently of their more special cognitive abilities (Snow, Kyllonen, & Marshalek, 1984). Figure 35.1 shows both an easy and a difficult example of Raven scale items. They must be solved quickly, as the full test consists of many such items and has to be completed in a limited time. These items have been designed so that their solution is unlikely to be influenced by previous knowledge that individuals might or might not have. The scales are constructed so that even extended experience with one version of them has only a negligible influence on how well one performs with the next version of them. The fact that the intelligence gauged by such tests is an ability that cannot be easily taught and learned is undoubtedly the source of widespread uneasiness. What the test measures is often felt not to correspond with the everyday connotations—whatever they precisely are—of the term *intelligence* (Lenz, 2000). Many textbooks of cognitive psychology avoid the subject of individual differences in cognitive competencies, perhaps because of political correctness (e.g., Matlin, 2002; Medin, Ross, & Markman, 2001; but see Solso, MacLin, & MacLin, 2008; Sternberg, 1996). The notion of innate individual differences seems to go against the fact that experience can improve one's performance with tasks such as improving texts or assembling furniture. Furthermore, some of us seem inherently good at drawing (or mathematics), but inherently poor at writing (or singing). We will return to these issues later.

Animal Intelligences

Even before Darwin (1809–1882) proposed that one must look for the roots of human intellect in animals, their intelligence was of much practical interest. For example, shepherds and cowboys were already well aware of the differences in working intelligence among individual collies or horses. Older members of the senior author's laboratory still remember one extraordinary pigeon that could solve complex behavioral tasks within hours or days, problems that other pigeons would not solve within weeks or months. Because they are after universals rather than particulars, animal behavioral scientists have nevertheless largely ignored the interindividual variations in cognitive capacities of their subjects (but see B. Anderson, 2000; Matzel et al., 2003). Banerjee et al. (2009) have more recently analyzed the interindividual differences in performance of tamarin monkeys on a series of cognitive tasks and plausibly attributed a part of the interindividual performance variance to a general intelligence factor. In siskins, small songbirds, it has been found that their individual ability to solve a foraging problem is correlated with their individual plumage colorfulness (Mateos-Gonzalez, Quesada, & Senar, 2011; cf. Kanazawa & Kovar, 2004).

On the whole, intelligence differences between species have been more commonly, though by no means universally (cf. Macphail, 1978), accepted. Anyone watching macaque rhesus monkeys and pygmy chimpanzees at the zoo for an adequate length of time is likely to be sure that the latter are

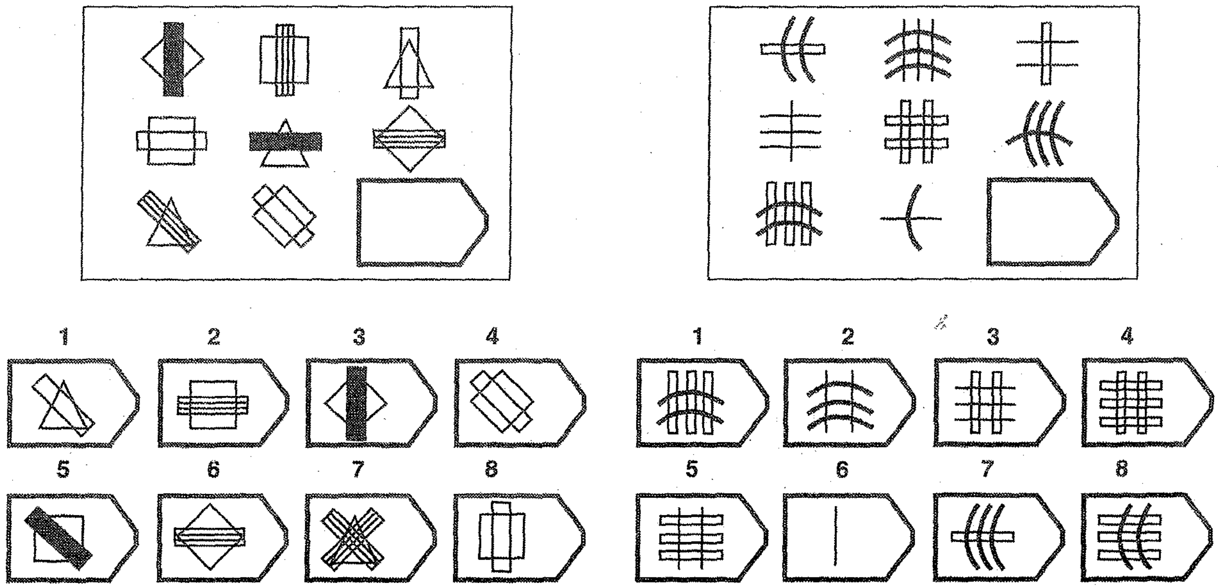

Fig. 35.1 An easy item and a difficult item from the Raven intelligence scales. The gaps must be filled with one of the panels offered. (based on Carpenter, Just, & Shell, 1990).

more intelligent than the former. Indeed, Deaner, van Schaik, and Jonson (2006) have quite objectively established that apes cognitively outperform monkeys—by comparing how well they coped with a series of different behavioral tasks. Similar considerations also pertain to judgments about differences between more gross phyletic groups, such as birds being generally rated more clever than fish (Nakajima, Arimatsu, & Lattal, 2002). Note, however, that all of these comparative intelligence judgments effectively derive from a collective evaluation of achievements on an assortment of behavioral problems. It is undeniably the case that the design of a succinct and universal test of animal intelligence has turned out to be difficult, an issue to which we now turn our attention.

Learning Sets

Harry Harlow (1905–1981) and colleagues attempted to assess the intelligence of various species by judging how well they would acquire learning sets. The learning-to-learn procedure they used involved challenging individual animals with a series of discrimination learning problems, all of which were procedurally identical, but each involved new stimuli. For example, macaques first had to learn in repeated trials that lifting a toy car rather than a simultaneously presented toy airplane would reveal a hidden peanut reward. Next, they had to learn that a cup, but not a can, signaled reward, and so on with a number of "junk object" pairs. The animals initially took a considerable number of trials with each pair of new objects before consistently picking the rewarded one, but, by about the 100th pair, the macaques had learned to choose correctly by the second trial with each novel pair (Warren, 1973). It was found that some species, foremost chimpanzees, showed near-perfect discrimination on the second pair after experience with only about a dozen stimulus pairs (Schusterman, 1964). Other species, such as the rat, showed only minor improvements in this learning-to-learn task. The latter species were accordingly considered to be less intelligent than the former. Most 6- to 7-year-old schoolchildren are quicker than chimpanzees at acquiring this optimal strategy, needing only pre-experience with two or three pairs of stimuli, but apparently it has not been examined whether the individual performance of children on this kind of task correlates with their test intelligence (S. Buschio, personal communication). Paule, Chelonis, Buffalo, Blake, and Casey (1999), however, found a link between test intelligence and performance accuracy on tasks of an even simpler kind. Learning-set tasks can be viewed as the learning of a special expertise that helps to solve a particular kind of problem, but it is not quite what human intelligence tests attempt to measure (see later). Some work has been done on the learning-set task with non-mammalian species, and some bird species have done quite well (Kamil, Lougee, & Schulman, 1973; Plotnik & Tallarico, 1966; cf. Helton, 2008, about foraging expertise acquisition in a variety of animals).

There are data on a somewhat wider range of species for another task of a similar but simpler nature: serial reversal learning (Warren, 1973). Subjects learn to discriminate a pair of stimuli as before, but once they have acquired the discrimination, instead of being confronted with a new pair, they continue with the same pair, now with the contingencies of reinforcement reversed. That is, if choices of A were rewarded and choices of B were not rewarded previously, choices of B are now rewarded and choices of A are not. When the subjects have learned to respond adequately to this reversal, the reinforcement allocation is reversed again, and so on. A cognitively gifted species can be expected to learn to behave according to the rule, "if a stimulus ceases to yield reward, switch to the other stimulus on the next trial." Indeed, most macaques manage to adopt such a strategy within a few reversals. Pigeons show improvements in learning the successive reversals, but never achieve such an immediate switching strategy (Delius, Ameling, Lea, & Staddon, 1995; Diekamp, Prior, & Güntürkün, 1999; Staddon & Frank, 1974). Some other bird species performed better on this task, achieving levels comparable to those of monkeys (Bond, Kamil, & Balda, 2007; Gossette & Gossette, 1967). Of a sample of 20 university students, many achieved nearly rule-like behavior after five reversals on a task involving the concurrent discrimination of two pairs of irregular polygons. However, a few students did not exhibit any significant performance improvements. Remarkably, among the successful students, several could not verbally explain at all what rule they had finally used (Siemann, von Selzam, & Borchert, 2004; see later).

According to an early study, rats show comparatively little learning-to-learn ability (Warren, 1973). The rats had been trained to jump toward a pair of doors bearing different visual patterns, such as a triangle and a circle. The door displaying the triangle would, for example, be designated correct and open to give access to a food reward. The other, displaying the circle, would be the incorrect one and would be locked, the rats falling onto a net as a penalty. However, rats are night-active animals and are not well adapted for the recognition of visual patterns in daylight. When Slotnik and Katz (1974; see also Slotnick, Hanford, & Hodos, 2000) used different odors as stimuli and arranged a more suitable procedure, they found that rats were considerably more capable than originally judged. Unsurprisingly, rats were better with stimuli that they are better equipped to recognize. One can expect that humans, being relatively microsmatic, would conversely do worse on an olfactory test than on a visual test, even if the odors were chosen to be discriminable for them (cf. Danthiir, Roberts, Pallier, & Stankow, 2001). The point is that it is hard to design a testing situation that is sufficiently uniform to yield comparable measures while being equally appropriate to the perceptual, motivational, and motoric dispositions of species that are adapted to quite diverse environments. The difficulties are not unlike those arising when human psychologists attempt to design intelligence tests that are also fair to motorically disabled or blind persons. The upshot of this conundrum is that behaviorists have largely given up trying to design a universal animal intelligence test. They have rather turned to examining the performance of animals on a wider range of cognitive tasks (Reznikova, 2007; Wasserman, 1993; Zentall, 2000).

Concept Formation

Being able to group different perceptual items under one cognitive category is undoubtedly a basic prerequisite for intelligent information processing. Humans' singular ability to form multifarious concepts is considered an essential element of our intellectual superiority. Interestingly, though, as research on humans has progressed, it has become ever less certain how concept formation should be operationally defined (Murphy, 2002). A capacity of categorizing items of somewhat diverse appearances as belonging (or not belonging) to a class is certainly a precursor to concept formation (cf. Freedman & Assad, 2006; Peelen, Fei-Fei, & Kastner, 2009). Thus, we can recognize animals such as canaries, hummingbirds, penguins, and owls as belonging to the class of avians because they are all feathered and have a beak, two legs, and a pair of wings. It is well established that monkeys and pigeons are capable of similar classificatory feats, but it is less well established whether, for example, rats can do so, perhaps because human experimenters find it difficult to design corresponding tasks within the olfactory realm (Herrnstein, 1990).

A more abstract classification applies when humans, for example, group very different-looking animals such as snails, aphids, geese, manatees, and giraffes as belonging to the class of herbivores on the basis of what they eat. This kind of item grouping is viewed as an instance of true concept formation (Sloman & Rips, 1998). Anagenetically advanced animals can associate different stimuli according to analogous functional criteria (Astley & Wasserman, 1999; Zentall, 1998). We ourselves have investigated the issue by training pigeons to discriminate two pairs of different-looking stimuli A+C- and B+D-, where + and - signify that the choice of the corresponding stimuli out of serially randomly presented pairs was rewarded and not rewarded, respectively. When the birds had learned to choose the positive stimuli, the reinforcement allocations were reversed: A-C+ and B-D+. As soon as the pigeons had switched their stimulus preferences, the reinforcement allocations were again reversed, and so on several times, until the birds had learned to quickly alter their stimulus choices. The birds were then tested to determine whether they had formed two functional classes involving the stimuli such that if A was rewarded in a given session, B would be rewarded too, and if C was rewarded in another session, D would also be rewarded. For this test, a reinforcement reversal would begin with only one of the pairs being shown until the birds switched their choice behavior to it (the leading pair); only then would the other stimulus pair be presented (the trailing pair) to assess transfer of the choice reversal.

Figure 35.2 shows how well pigeons performed on the first three presentations of the leading pair after the reversal and how well they did on the first three trailing-pair presentations after they had mastered the current reinforcement allocation on the leading pair. It is apparent that they did far better, though by no means perfectly, with the second pair than with the first pair (Delius, Jitsumori, & Siemann, 2000). This finding demonstrates that, because of the stimulus equivalencies learned, the pigeons could transfer short-term information acquired with the first pair to solve the task posed by the second pair. Using a more sophisticated version of the reversing reinforcement allocation and eight different stimuli, we could demonstrate that pigeons were able to conceptualize them as belonging to two different equivalence classes. We then added further stimuli to build up a network of equivalencies. The more capable pigeons—individual variations proved to be important here—were able to associate stimuli

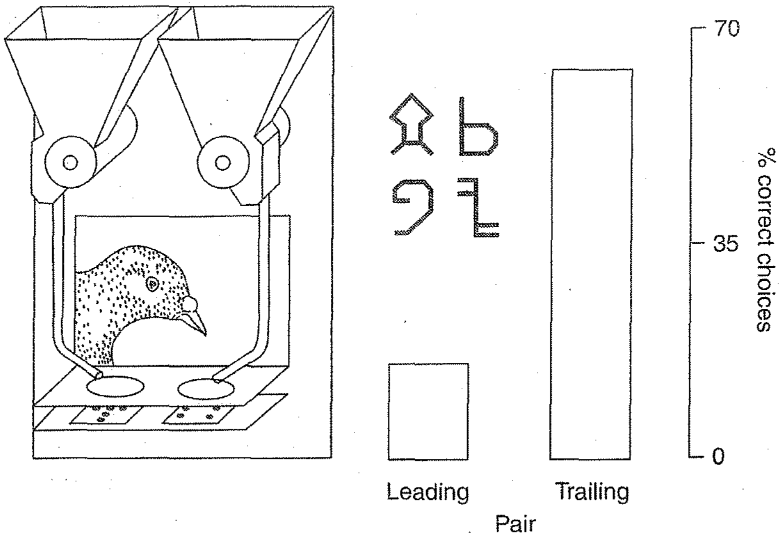

Fig. 35.2 Concept formation according to functional equivalencies in pigeons (modified from Siemann, von Fersen, & Delius, 1998).

by their conjoint property of switching from yielding reward to yielding nonreward and back again (Jitsumori, Siemann, Lehr, & Delius, 2002; cf. Jitsumori, Shimada, & Inoue, 2006).

Von Fersen and Delius (2001) taught two bottlenosed dolphins the basic serial reversal task with two stimulus pairs. The dolphins easily succeeded in discriminating the visual stimuli, but they never showed any reversal transfer from one pair of stimuli to the other as the pigeons had done. However, when four auditory stimuli were used, the dolphins easily acquired the equivalence relations among them. With the auditory stimuli, their performance was better than that of the pigeons with visual stimuli. It is very unlikely that pigeons would perform better with auditory stimuli than with visual stimuli, as they are more adept at cognitively processing visual stimuli than auditory stimuli (Delius & Emmerton, 1978). It seems likely that much as rats were earlier suspected to be more cognitively capable with olfactory than with visual stimuli, dolphins may be more intelligent when dealing with auditory than with visual stimuli (Roitblat & von Fersen, 1992).

Siemann et al. (2004) found that although university students were naturally more efficient than pigeons or dolphins at learning the basic discriminations constituting the serial reversal task, they still varied individually in their ability with tests involving equivalence class transfer. The students also differed considerably in their awareness of the task's logical structure, but the relation between the students' transfer performance and their test intelligence was not examined. Experiments using a different methodology have shown that mentally handicapped schoolchildren have considerably more difficulty forming equivalences than same-age controls (Sidman, 1992). In any case, these studies suggest that some behavioral tasks with which at least some birds and mammals can cope also challenge the cognitive competencies of younger or less-gifted humans, even if it is not clear whether these competencies are those measured by intelligence tests.

What is obvious, however, is that the uniform assessment of the intelligence of animal species is made difficult by the different specializations that the various species have evolved. It is reasonable to speculate that the olfactory intelligence of rats is linked to their nocturnal way of life and that the auditory intelligence of dolphins is related to their sonar mode of orientation (Shettleworth, 1998). Similar ecological arguments have been proposed in connection with the presence of an enhanced memory competency in bird species that cache surplus food in many different locations for later, leaner times (Krebs, 1990; but see Macphail & Bolhuis, 2001; cf. Healy, de Kort, & Clayton, 2005; Osvath, 2009). Indeed, this faculty appears to be associated with a relative enlargement of the hippocampus, a brain area that appropriately, among other things, is known to be involved in encoding the spatial layout of the environment. However, it is not altogether certain whether the latter enlargement is not a secondary ontogenetic adaptation (cf. Ekstrom et al., 2003; Maguire et al., 2000).

Transitive Responding

It is not immediately obvious that if $x < d$, $m > d$, and $f < x$, then it must follow that $f < m$. The more terms that are involved and the less well ordered the premises that are presented, the harder it is to draw the correct conclusions. Transitive inference problems of a similar nature have been designed so that they can be given to very young children or, indeed, to animals. In the simplest case, they learn over many trials to discriminate concurrently four overlapping pairs of five stimuli, A+B-, B+C-, C+D-, and D+E-, randomly ordered, until they achieve a criterion level of choice accuracy. Then, animals and children are presented with a test pair of stimuli not previously presented together, BoDo, without reinforcement (0) for their choice. If the subjects interpret the task in terms of a transitive inference problem (A > B, B > C, C > D, D > E), then they should prefer B to D. In fact, that is what subjects actually do (children, squirrel monkeys: Chalmers & McGonigle, 1984; pigeons: von Fersen, Wynne, Delius, & Staddon, 1991; cf. Fig. 35.3). Note that all three species did about equally well with test pair BoDo. However, the pigeons took longer to learn the premise pairs than the monkeys, who took longer than the children. All the same, Lazareva and Wassermann (2006) have shown that the transitive B > D choices of pigeons are not the mere product of a protracted conditioning process.

Siemann and Delius (1998; see also Delius & Siemann, 1998) conducted analogous experiments with students. As reinforcements for correct and incorrect stimulus choices, students gained or lost symbolic coins. The students learned the premises far faster than pigeons or indeed children, but they were not much better on the conclusion pairs. When faced with the test pairs, two thirds of the students did quite well, but about one third of the students chose randomly. Interestingly, these failures were not linked with lower test intelligence. Rather, it appeared that these individuals had learned to correctly respond to the various stimulus pairs (AB, BC, etc.) as compound patterns without attending to the fact that the component elements (B, for example) recurred in different pairs. When later faced with BoDo conclusion pairs, these students did not have any ready response to these new compound stimuli. It is likely that an enhanced capacity for configural perception is a part of human intelligence (Matsumoto, Ohigashi, Fujimori, & Mori, 2000), but it was counterproductive here because it could not provide the information needed to solve the problem.

Questionnaires after the experiment revealed that about half of the students who solved the test pairs were aware of the logical structure of the inference task but the other half were not. Nevertheless, the students with an explicit understanding did not perform better than did the ones without. We assume that the former—despite knowing about the principle on which the task was based—could not bring this explicit knowledge to bear because of the requirement to choose as fast as possible (cf. Greene, Spellman, Dusek, Eichenbaum, & Levy, 2001). The deliberative reasoning that would be needed is a relatively slow process that could not be

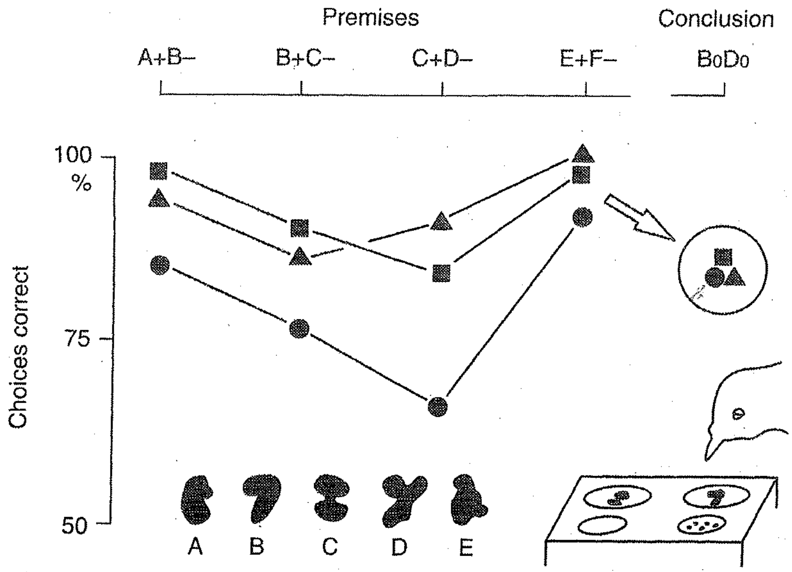

Fig. 35.3 Transitive responding in pigeons, squirrel monkeys, and humans (based on Siemann, von Fersen, & Delius, 1998).

applied within the short reaction times recorded (about 1 second; cf. Leighton & Sternberg, 2003). Indeed it appears that the transitive inference problem presented here mainly challenges the efficiency of longer-term learning mechanisms rather than the quality of the working memory system with which intelligence tests are mainly concerned (see later). Nevertheless, it is remarkable that pigeons could outperform humans on this task. By the way, in an experiment that did not demand especially speedy responding and using stimuli that invited verbal naming, Martin and Alsop (2004) found that the transitivity performance of human subjects was indeed related to the extent of their problem awareness.

Just as primates stand out intellectually among mammals, parrots and corvids tend to stand out among birds. The productive language feats by African grey parrots (Pepperberg, 1999, 2006) and the insightful problem solution by American ravens (Heinrich, 2000; cf. Emery & Clayton, 2004; Weir, Chappell, & Kacelnik, 2002) can only be usefully compared with performances by apes; not even monkeys do as well. One can find antecedents of particular competencies in pigeons (e.g., Nakajima & Sato, 1993; Xia, Emmerton, Siemann, & Delius, 2001), but the ease with which parrots and corvids cope with many tasks that are difficult for pigeons must be stressed (Mackintosh, Wilson, & Boakes, 1985). Note that corvids and parrots are related by deriving from a shared ancestral passerine (songbird) lineage (Hackett et al., 2008). More generally stated, birds often turn out to be on par with mammals regarding specific intellectual competencies. Birds certainly stand above reptiles, amphibians, and fish, for which competencies like learning sets, concept learning, or transitive responding are borderline or absent (but see Brown, Laland, & Krause, 2006; Bshary, Wickler, & Fricke, 2002; Grosenick, Clement, & Fernald, 2007; Leal & Powell, 2011). This picture appears to be true despite the fact that Macphail (1987) has argued that all vertebrates except humans are of about equal intelligence.

Rotation Invariance

A kind of item that appears in several human intelligence and ability tests involves a spatial skill known as mental rotation (Eysenck, 1990). An example is shown in the lower inset of Figure 35.4. Subjects have to identify which one of the various patterns shown deviates by being a mirror image of the others. The accuracy and speed with which individual humans solve such items correlate highly with their test intelligence (Kail & Pellegrino, 1985). A related procedure has been used to assess the mental rotation abilities of both animal and human subjects. For pigeons, three stimuli were presented side by side and one or the other of the lateral stimuli was odd with respect to the middle stimulus (see upper inset in Fig. 35.4). Pigeons first learned that pecking the odd lateral stimuli yielded food reward. This was always the mirror image of the sample stimulus. Choices of the sample-identical lateral stimulus were penalized with a period of darkness. It was important that the birds learned to perform this task with several different visual shapes to ensure that they had acquired a general preference for the mirror stimuli. Pigeons were earlier thought to be unable to learn such an "always choose odd stimulus" rule, but it is now clear that they can do so under propitious conditions (Bodily, Katz, & Wright, 2008; Cook, 2002; Lombardi, 2008).

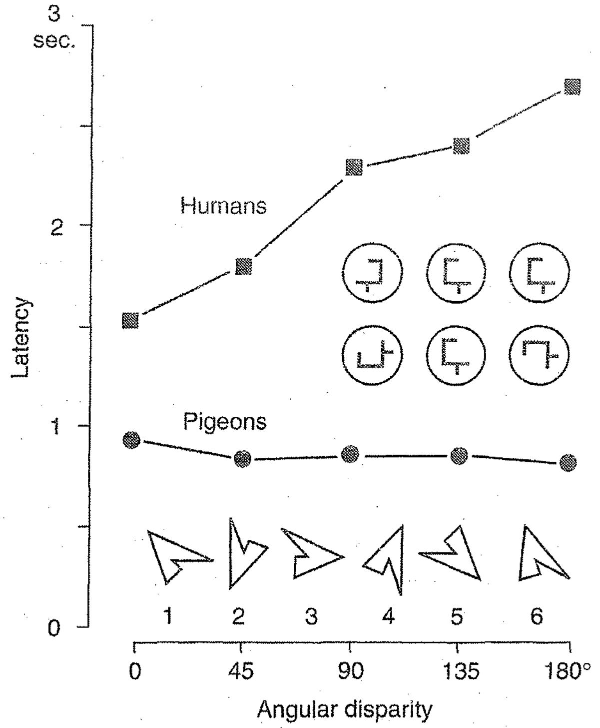

Fig. 35.4 Mental rotation in humans and pigeons. *Lower inset*: Item out of a human intelligence test; subjects have to identify which one of the various patterns shown deviates by being a mirror image of the others. *Upper inset*: Present experiment with humans and pigeons; three stimuli were presented side by side and subjects had to identify which of two lateral stimuli was odd with respect to the middle stimulus (based on Eysenck, 1990, and Hollard & Delius, 1982).

The test stage involved presenting both comparison stimuli rotated by the same angle relative to the sample stimulus. Apart from the 0-degree training disparity, the pigeons were tested with 45-, 90-, 135-, and 180-degree sample-comparison disparity triplets. The tests showed that the pigeons made about the same number of errors, about 10%, and took about the same amount of time (just under a second) to choose, regardless of the varying orientation disparities (Fig. 35.4; Hollard & Delius, 1982; Lombardi, 1987). It needs to be stressed that this result does not mean that pigeons are invariably insensitive to the orientation of visual patterns, as some critics seem to have assumed (e.g., Hamm & Matheson, 1997). In differently designed experiments, we ourselves showed that, under different circumstances, pigeons are quite sensitive to orientation differences (Lohmann, Delius, Hollard, & Friesel, 1988). A related alternative responsiveness or nonresponsiveness to pattern orientation disparities could, by the way, also be demonstrated in humans (Förster, Gebhard, Lindlar, Siemann, & Delius, 1996).

Much the same rotation invariance experiment was carried out with students. They received money instead of food for correct choices. With the help of verbal instructions, the students needed only a few training trials with the 0-degree disparity trials. In terms of errors, they did slightly better than pigeons in test trials. However, they were generally slower in choosing and took longer as the orientation disparity between sample and comparison stimuli was greater. This finding replicates the typical results of many mental rotation experiments with humans (Delius & Hollard, 1995). Some people can mentally rotate quickly and produce shallow reaction functions, while others can only mentally rotate slowly and produce steep functions. This rotation speed correlates appreciably with their test intelligence. However, no human seems to be able to mentally rotate as fast as pigeons can. In this very narrow respect, pigeons are more test-intelligent than humans (cf. C. Köhler, Hoffmann, Dehnhardt, & Mauck, 2005, about rhesus monkeys).

Why are pigeons so good at mental rotation problems while humans are not? The likely distal explanation is that there is considerable selection pressure on pigeons to recognize objects regardless of their orientation with reference to the observer, whereas there is far less such pressure on humans. This selection pressure has to do with the fact that pigeons, from their pronate stance, predominantly look down on the horizontal ground plane, where objects have no standard alignments vis-à-vis observers. In contrast, humans, from their upright stance, look predominantly at frontal, vertical planes, where objects and observers tend to have fixed orientations due to gravity. As to a proximal explanation, computational analyses of the information processing required for such invariant recognition show that both a serial and a parallel processing strategy are viable. The former is economical in terms of processing units but slow and error-prone when large orientation disparities have to be bridged (human performance), whereas the second is insensitive to increasing degrees of disparity but expensive in terms of processing units (pigeon performance; Delius, Siemann, Emmerton, & Xia, 2001). Furthermore, the parallel processing circuitry must be tuned to the particular task, but the serially processing circuitry—more amenable to reprogramming—can probably be used in other cognitive tasks. This difference is perhaps what underlies the distinction between special abilities and general intelligence treated later.

Evolving Intelligence

How did intelligence evolve as the property of a few organisms and not of many others? The key protagonists of biological evolution are ribonucleic acid molecules. As soon as they arose from precursor organic molecules about 4.5 billion years ago, they began to play the evolutionary game (Dawkins, 1989). They did this because of their unique capacity of nearly perfect replication. From the very beginning, the persistence and multiplication of these molecules—that is, their Darwinian fitness—would have been threatened by inimical environmental conditions. Their replication rates were dependent on their capacity to requisition material and energetic resources from the environment. Different variants of these gene molecules turned out to be more efficacious than others in different environmental niches. The gene variants arose because of a not-altogether-perfect replication (i.e., their capacity for mutation). Over billions of generations, this process led to the appearance of millions of different species of organisms, only some of which still populate the Earth. Genes of organisms that could synthesize a protective envelope, a soma, for themselves at some point of this biological history were at an advantage over those that could not. Their cellular membrane enclosed the cytoplasm, an interposed *milieu interieur* that buffered the genes from the harshness of the environment (Futuyma, 2009).

Pluricellular organisms evolved mainly because they achieved an improved encapsulation of the inner environment. Later in evolutionary history, genes that could instruct the synthesis of structures that ensured a physicochemical reactivity would be selected in some species because they allowed individual adaptation to unstable environments. The adaptability of individuals among species inhabiting spatially varying environments would be enhanced by the emergence of mutants phenotypically capable of sensing promising niches and growing into them. Mutants capable of instructing mechanisms that ensured motility would perfect the competence to seek fitness-promoting environments.

In the beginning, all behavioral responses to sensed events would have been genetically, innately determined. Some pluricellular organisms underwent mutations that would lead to cellular networks exclusively dedicated to a signaling mechanism to mediate between sensory receptors and motor actuators (Bonner, 1988). A genome capable of instructing intercalated neurons that would enable these organisms to convert differing arrays of sensory inputs into varying patterns of motor outputs would have been beneficial. Proper nervous systems began to evolve. A set of mutant genes that allowed neural structures to adjust according to individual experiences would again have been advantageous to some organisms, given the right circumstances. The capability for learning and memory had emerged. Any genes that instructed mechanisms enabling a more rapid information processing, detection of ever-more-complex interrelationships between stimuli, allowing the storage of these associative complexities, and ever-more-differentiated manners of responding to them might again provide a selective advantage in some socioecological niches. A property that one might be inclined to call intelligence would have arisen (Bullock, 1993; Heschl, 1998).

Note that, at every stage of this sketch of the progressive, anagenetic evolution of intelligence, there is always the qualifier that the right circumstances had to apply for the selection of improved cognitive abilities to occur. Of the million or so species that exist on earth, only a very small proportion is capable of showing any behavior, an even smaller proportion capable of any learning, and only exceedingly few qualify as possibly intelligent. The influenza and HIV viruses do very well with no behavior at all, liver flukes and sea urchins thrive despite the fact that they are virtually incapable of any learning, and the common toad and the stickleback fish manage fine without much intelligence. There is hardly any doubt that occasional mutants have arisen in these organisms that might have provided them with some behavior, with improved learning and expanded intelligence, but probably the costs of such capabilities exceeded the benefits in terms of fitness. The price of intelligent behavior is grossly that of having more neurons and therefore larger nervous systems.

Of course, it is not only sheer brain enlargement that can bring overall information-processing improvements but also increased conduction speed, improved synaptic efficacy, augmented neural connectivity, more synaptic variety, novel neuron types, added neuron miniaturization, tighter neural packing, superior metabolic efficiency, pronounced hemispheric asymmetries, and so forth (Arbas, Meinertzhagen, & Shaw, 1991; Magat & Brown, 2009; Matzel, Gandhi, & Muzzio, 2000; Nimchinsky et al., 1999; Roth, Blanke, & Wake, 1994; Volman, 1990). The best example of the fact that cognitive cleverness is not a mere matter of absolute brain size are honey bees, whose abilities often approach and occasionally may even exceed those of avians and mammals (Chittka & Niven, 2009; Giurfa & Menzel, 2003). Still, much of the cleverness of social insects is more the product of the cooperative functioning of their colonies than of the cognitive capacities of individuals (Franks, 1989). By and large, however, significantly increased information-processing capacities can arise only from a large and complex brain. But of course, these capacities have to develop meaningfully during individual growth, have to be metabolically maintained in adulthood, and, not the least, have to be carried around. In many of the varied environmental contexts in which the members of most species find themselves, the fancier brains afforded by advanced intelligence would simply not result in an overall, net fitness advantage (Delius et al., 2001; cf. Isler & Van Schaik, 2009; M. Köhler & Moyà-Solà, 2004; Scott, Jones, & Wilkinson, 2006).

Intelligent Brains

It is important to realize that it is the selection pressure for more varied behavior, improved learning, and expanded intelligence that brings about the evolution of more voluminous and more sophisticated brains. It is not, as some have suggested, due to some intrinsic drive that makes brains ever larger and more intricate and then allows them to produce increasingly complex and refined behavior. The first requirement is the chance appearance of gene mutations that enable the ontogenetic development of a brain with improved cognitive capabilities. The probability of any odd mutation leading to such improvement is low. For it to be effective, the mutation must first fit in with the preexisting genome.

For it to spread through the population, it is a requisite that the socioecological circumstances be such that the enabled intelligent behavior brings about a fitness advantage to the individuals displaying it. This advantage entails that, in the course of evolutionary time, the genome of some species—but definitely not that of others—ended up instructing the development and maintaining the functioning of large and complex brains (Striedter, 2005). Note though that, in terms of sheer numbers, the microcephalic and unintelligent tuna fish, for example, are still doing considerably better than the nearly same body-sized but macrocephalic and intelligent chimpanzees.

Figure 35.5 summarizes the relationship between body and brain weights of vertebrates. Generally speaking, small animals have small brains and large animals have large brains, mainly because a larger body mass necessarily incorporates more sensory, secretory, and motor elements that need to be interconnected (Jerison, 2001). However, the oblique polygons that enclose the brain weights of birds and the brain weights of mammals in Figure 35.5 lie above those that enclose the brain weights of reptiles. Within the mammalian polygon, open circles represent the brain weight of a selection of nonhuman primates, which obviously lie somewhat above the remainder of the mammals. The filled circle represents the human species. Within the avian polygon, the open squares, representing a few species of corvids and parrots, similarly lie in its upper half (cf. Cnotka, Güntürkün, Rehkämper, Gray, & Hunt, 2008). The polygons corresponding to amphibian and fish species (not shown) overlap closely with that of the reptiles. Thus, the relative brain weights correspond to the assumed intelligence rankings informally assigned to the various vertebrate groups (Van Dongen, 1998). Even within the human species, the brain sizes of individuals correlate weakly, but significantly, with their test intelligences (Deary, 2000; McDaniel, 2005). Size differences of some component brain structures probably have a more marked impact (Deary, Penke, & Jonson, 2010). That the size and structuring of brains can be shaped by the bioevolutionary process relies on the fact that both characteristics are under considerable genetic control (Cheverud et al., 1990; Kaschube, Wolf, & Geisel, 2002; Thompson et al., 2001).

The large relative size of the human brain is principally due to our relatively oversized forebrain. The highly convoluted folding of the human telencephalic cortex is its salient feature. The convolution has to do with an increased number of cortical columns, thought to be the elementary neural networks that implement cortical processing (Fuster, 2002). The folding is apparent in several mammalian groups, but in primates and especially in humans it is particularly pronounced (Rehkämper, Frahm, & Mann, 2001). Still, cortex volume and folding are not invariably indexes of intelligence. Dolphins are endowed with a remarkably large and folded cortex, but its neuron and neuropil densities are remarkably low. Indeed, the intelligence of dolphins, thought a few years ago to be on par with that of apes, has lately been judged—even if controversially so—as not so particularly outstanding (Manger, 2006; cf. Deaner, Isler, Burkart, & van Schaik, 2007; Kingsbury, Rehen, Contos, Higgins, & Chun, 2003). Still, the

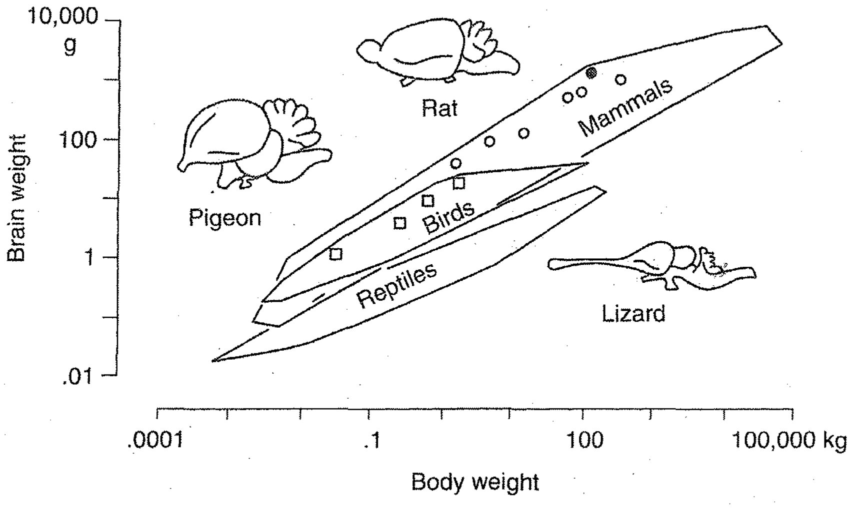

Fig. 35.5 Brain weights as a function of body weights in reptilian, avian, and mammalian species. The inserts illustrate the brains of a rat, a pigeon, and a lizard, all three species having about the same body weight (based on van Dongen, 1998).

larger dolphins and whales are anything but dumb: they may be benefiting from the absolute size of their brains giving them a straight advantage of scale; the same may apply to elephants (cf. Plotnik, Lair, Suphachoksahakun, & de Waal, 2011).

It is now accepted that birds possess an overgrown dorsal pallium that is analogous to the mammalian neocortex and makes up a considerable portion of the avian telencephalon (Butler & Hodos, 1996; Jarvis et al., 2005; Reiner, 2009; Veenman, 1997). The small dorsal pallium of reptiles is assumed to be the structural predecessor of both the avian and the mammalian cortex. However, the avian cortex does not possess the tidily layered and columnar organization typical of the mammalian neocortex. But, as well known to electronics technicians, a superficially not-so-tidy circuit can function just as well as one that is tidier. Indeed, if very fast signal processing is at a premium, then an apparently disorderly circuit can have an edge over an obviously better-ordered one. Birds even appear to have a cortical area that is equivalent to the prefrontal cortex of mammals, a structure that, as discussed later, is central to human intelligence (Aldavert-Vera, Costa-Miserachs, Divac, & Delius, 1999; Güntürkün, 2005; Kirsch et al., 2009; see also Wild & Williams, 2000).

But probably neurobiologists have been too focused on cortical brain structures when considering the neural substrates of cognitive performance in the past (Parvizi, 2009). Birds also posses a voluminous cerebellum that is as complexly structured histologically as that of mammals (Dubbledam, 1998). The cerebellar cortex, at least in humans, is not, as classically assumed, solely dedicated to the coordination of movements but is also involved in cognitive functions that contribute to intelligence (Hogan et al., 2011; Schmahmann, 1997; Spence et al., 2009). Birds, moreover, possess the most tidily layered and neatly columnar neural structure found anywhere. Santiago Ramón y Cajal (1852–1934) listed some 14 neuronal layers in the optic tectum of birds, whereas he only recognized about 6 in the cerebral cortex of mammals. But it must be conceded that there is only meager evidence that the optic tectum participates in intelligent information processing (Hardy, Audinat, & Jassik Gerschenfeld, 1987; Hellmann, Manns, & Güntürkün, 2001; Wiltschko & Wiltschko, 2002). Nevertheless, in principle, birds are neurally very well equipped for complex information-processing operations.

Inasmuch as intelligence is a characteristic that transcends the elementary capacity for efficient learning and is best captured by the range of cognitive operations of which a given species is capable, birds and mammals are a league above that of all other animals. On a geological scale, the origins of intelligent behavior would therefore go back to the early Permian period, about 300 million years ago, when the ancestors of birds, the theropodans, branched off. The small arms of some of these dinosaurs evolved into feathered, although still clawed, appendages. These feathered arms probably assisted in the fanning-in of volatile prey while jumping upward and forward. By the time proper birds had evolved in the early Cretaceous era (about 150 million years ago), true wings enabled flight (Alonso, Milner, Ketcham, Cookson, & Rowe, 2004; Feduccia, 1996; Zhou, Barrett, & Hilton, 2003). This energy-demanding motor activity was dependent on a level of metabolic turnover that only a regulated body temperature could ensure. Homeothermy would arise, and this in turn would open the way to an efficient utilization of the nervous system. The therapsids, the saurian ancestors of mammals, branched off soon after the theropodans, about 280 million years ago. The mammals that derived from them about 180 million years ago went on to occupy a nighttime niche where they did not have to compete with the reptiles but where homeothermy was an imperative requirement. The renewed emergence of homeothermy entailed another flourishing of behavior potentialities among mammals (Gisolfi & Mora, 2000; Ruben, 1995).

The relative intellectual backwardness of fishes, amphibians, and reptiles is largely ascribable to the fact that they remained poikilothermic. Even if simpler neural functions, such as action potential conduction, are not impeded by this condition, other functions such as synaptic transmission and synaptic plasticity may be (Janssen, 1992). Lethargy at lower temperatures certainly restricts the possibility that intelligent behavior might have an impact on evolutionary fitness. In mammals and birds, however, warm-bloodedness ensured that intelligent behavior would acquire crucial importance. The large and intricate brains that resulted gave rise to the evolution of extended and involved styles of parental care; these in turn demanded more sophisticated behaviors and brains. A runaway evolutionary process began to operate that, however, could never quite escape the surplus costs of having larger brains.

Social Intelligence

The course of evolution is importantly shaped by chance events. Not only is the emergence of mutations a stochastic process, but also their selection is often determined by haphazard events. The evolution of mammals and birds was in all probability critically influenced by the sudden extinction of the dinosaurs and other large reptiles due to the impact of a very large meteorite about 65 million years ago (Lyson et al., 2011). The growth of tropical forests caused by climate changes in the aftermath might have promoted the evolution of primates about 50 million years ago. This environment offered spatially and seasonally patchy food supplies: trees bearing fruit here and there, now and then. That uncertainty favored the emergence of socially organized groups. Competition within the groups would become the prime selective agency affecting the behavior of ancestral primates. This is what the Machiavellian theory of primate intelligence basically proposes (Byrne, 1995; Flinn, Geary, & Ward, 2005; Whiten & Byrne, 1997; cf. Bond, Kamil, & Balda, 2003; von Bayern & Emery, 2009, about corvid birds).

What advanced the evolution of primate intelligence was less the harshness of the environment or the presence of predators than the intricate demands of social life. The fact that body-size-compensated whole-brain volumes—and more specially, cortical volumes—of mammals, and more so primates, are correlated with the size of the social groups they typically form accords with this hypothetical evolutionary scenario (Clark, Mitra, & Wang, 2001; Dunbar, 1998; but see Finarelli & Flynn, 2009; about birds, see Burish, Kueh, & Wang, 2004). It may also be symptomatic that several cognitive-reasoning problems are better solved by human subjects when they are posed within the context of a social interaction than when presented in a nonsocial format (Canessa et al., 2006; Cosmides, 1989; Gigerenzer, 1997).

The complexities of ape society have been aptly captured by the catchphrase "chimpanzee politics" (de Waal, 1988). The strategies that these apes use involve more sophisticated mental processes than those that they implement when coping with the physical environment (Povinelli, Reaux, Theall, & Giambrone, 2000). Shifting alliances and active deception are used, among other things, to further social status or to evade the consequences of low status (reduced access to quality feeding and mating opportunities, for example). In such contexts, apes appear to operate with some understanding of causality, some representation of the self, and some appreciation of the beliefs of others, competencies that are certainly less developed in monkeys (Call & Tomasello, 2008; Tomasello & Call, 1997; cf. Wojciechowski & Yosef, 2011, about house martins). Humans are, of course, well known to use many different strategies to alter the behavior of social partners to their own advantage. Even small children, some more cunningly than others, can use a variety of social bargaining techniques, such as alternatively endearing themselves, asking for more than they expect to get, or throwing a tantrum in public (cf. Klimes-Dougan & Kopp, 1999). The issue is complicated because strategies that might yield small gains in the short term may produce large losses in the long term. Aggressive behavior can yield immediate access to resources, but it can also prevent a lasting and more profitable friendly cooperation, thus compromising, for example, the advantage that groups can have over individuals when solving problems (Liker & Bókony, 2009; Seed, Clayton, & Emery, 2008; Yosef & Yosef, 2010). In any case, the ability to manipulate the behavior of others to one's own or one's group's advantage clearly involves special social skills (cf. Vignal, Mathevon, & Mottin, 2004).

Tests that attempt to assess individual differences in this social ability have been developed, but no really satisfactory measurement instrument has emerged. More importantly, the relevant tests do not reliably measure anything sufficiently different from what is assessed by cognitive intelligence tests (Kihlstrom & Cantor, 2000; Riggio, Messamer, & Throckmorton, 1991; but see Ramnani & Miall, 2004). The main difficulty is that problems requiring social operations cannot be as easily translated into formalized paper-and-pencil tasks as problems involving academic reasoning processes (see later). Nevertheless, it is notable that individual bargaining skills measured in game situations vary considerably and are correlated with personality characteristics when the interaction involved is simple, but with test intelligence when the interaction involved is complex (Barry & Friedman, 1998; Brandstätter & Königstein, 2001; see also Elfenbein, Curhan, Eisenkraft, Shirako, & Baccaro, 2006).

It is fashionable to hypothesize a separate and ancestral emotional intelligence (Goleman, 1995). When animals, including humans, behave emotionally, it functions predominantly to communicate to others their motivational state (Evans, 2001). An adequate externalization of emotional states is a necessity for successful social functioning. Howler monkeys with a pathological facial paralysis, characteristically, had great difficulty being accepted into their troop and were subjected to bouts of both excessive neglect and exaggerated antagonism (J. D. Delius, personal observations; cf. Coulson, O'Dwyer, Adams, & Croxson, 2004). Conversely, it appears that at least humans can vary in their ability to "read" the facial expressions of others (Sato, Uono, Matsuura, & Toichi, 2009). Among humans, a body-shove is interpreted as friendly if the perpetrator has a playful facial expression but as aggressive if he or she has a threatening facial expression. Additionally, emotional states can modulate the efficiency of cognitive functioning. Both fear and rage, for example, tend to paralyze rational reasoning (Salovey, Bedell, Detweiler, & Mayer, 2000). Our innate emotional constitution may be better adapted to life in earth-caves than to life in skyscrapers. It is conceivable that some individuals are neurally better equipped than others to neocortically control their limbic emotional states in socially or academically conducive ways (cf. Ledoux, 1998).

The difficulty with emotional intelligence is that, like social intelligence, there are no reliable instruments to measure it. Existing tests are only indirect questionnaires. A typical test item reads: "Assuming that the driver of the car in which you are traveling is angered by a supposed infraction of another driver, what would you do: (a) tell him to pipe down as the incident was of no consequence, (b) start playing his preferred music-cassette, (c) join him in cursing at the other driver, or (d) tell him that something similar happened to you and that on that occasion you found out that the guilty party was on his way to an emergency ward?" It is doubtful that any answer adequately gauges the subject's actual capability for emotional self-control. It is not even clear that what is being assessed is not just social intelligence and, indeed, whether the emotional intelligence trait is sufficiently distinct from that of general intelligence (Ciarrochi, Chan, & Caputi, 2000; Newsome, Day, & Catano, 2000; but see Mayer, Caruso, & Salovey, 2000).

Human Intelligence

Why are humans such particularly intelligent primates? A probable evolutionary scenario is that a lineage we have in common with chimpanzees and that occupied an arboreal niche had to cope with a freak climate change resulting in the savannization of east Africa about 5 million years ago. This change meant a forced shift away from a vegetarian diet to a carnivorous one. Note that chimpanzees, although still predominantly vegetarian, do occasionally also engage in communal hunts and eat meat (Goodall, 1986). Not being equipped with claws or fangs like longstanding carnivores, these prehominids had to employ tools such as spears and clubs. Some tool use in connection with feeding, although not with hunting, also occurs in chimpanzees. Initially, hunting could be successful only if it was carried out by social-intelligence–demanding cooperative gangs. Hunting-pack organization generated selective pressure for enhanced communication (Delius, 1990; Wilson, 1975; cf. Flinn et al., 2005; but see Gottfredson, 2007). The labeling property of language in turn improved intellectual functioning through an enhanced structuring of the mental representations of the world and the self. Language-trained chimpanzees and parrots outdo linguistically naïve peers in the performance of demanding cognitive tasks (Pepperberg, 1999; Premack, 1988). Additionally, by involving symbolic sequential operations, language required a serial mode of information processing that is not particularly natural for neuronal networks, which are more suited for parallel information processing (Nowak, Komarova, & Niyogi, 2003). The language faculty undoubtedly facilitated the evolution of a propositional form of information processing considered essential for the deliberative, rational reasoning needed to solve problems like those shown in Figure 35.1 (Carruthers, 2002; but see also Goldin-Meadow, 2003; Hespos & Spelke, 2004; see later). It is certainly no accident that a propositional mode of processing is frequently used in artificial intelligence programming (Russel & Norvig, 1995).

Practical Intelligence

Until advanced cultures began to emerge about 10,000 years ago, the cognitive problems that humans had to solve were of a practical, applied sort, not of an abstract, academic kind. Indeed, some of the dissatisfaction with intelligence tests arises because they seem divorced from everyday problem solving. The criticism is akin to that often raised regarding the nonecological nature of laboratory experiments on animal learning (Timberlake & Lucas, 1989; see also Gigerenzer, 1998).

As tests of practical intelligence, computerized games were introduced by Dörner and Reither (1978) to assess the managerial abilities of individuals. They involve subjects having to run a virtual factory. Several variables are related to each other through a varied set of equations. The input variables represent outlays (buying prime materials, investing in machines, paying personnel, borrowing money, etc.) and the output variables represent income (production volume, price level, etc.).

The subjects had to try to adjust the input variables so as to maximize the factory's profitability within an hour. The success of subjects in reaching this goal varied considerably and was found not to correlate with their test intelligence. Later studies, however, showed that this lack of correlation arose because the original factory games were not really rationally soluble within the time that the subjects had to play them. The performance differences arose because some subjects hit on good settings by chance and other subjects were not so lucky. When the games were modified to be more cognitively penetrable, a substantial correlation was observed between individuals' test intelligence and their purported management ability (Putz-Osterloh & Lüer, 1981; but see Berry & Broadbent, 1987).

Individual differences in managerial ability may exist, but they cannot be adequately measured with these factory games and they are unlikely to be totally divorced from test intelligence. Nor are they likely to be commensurate with individual differences in horse-race betting ability that were unearthed by another remarkable study of practical intelligence (Ceci & Liker, 1986). The wide range of practical abilities that have been looked into are not easy to subsume within one practical intelligence disposition, nor are they easy to separate from special abilities or, indeed, acquired expertise (Gottfredson, 2003; Sternberg et al., 2000; Sternberg & Grigorenko, 2002).

It is nevertheless widely accepted that there are a number of special intellectual abilities, such as verbal, spatial, or mathematical, that are at least partially independent of general intelligence. Indeed, many intelligence tests, as, for example, the Binet and Wechsler tests, include a proportion of items that tap some of these special abilities (Lohman, 2000). However, the assessment of these abilities often requires special instruments: Musical ability, for example, because it is not properly measurable with a paper-and-pencil test alone, requires an additional tape recorder. Further on this theme, although developers of intelligence tests soon recognized the desirability of including an assessment of the creative abilities of individuals, a reliable measure of this competence, beyond a fraction that is already represented in the general intelligence score, has proved elusive (Glover, Ronning, & Reynolds, 1989; Simonton, 2007; about innovative abilities in animals, see Ramsey, Bastian, & van Schaik, 2008).

The term *abilities* that is habitually used reflects a persisting doubt as to whether all these competencies refer to true separate intelligences or are merely special skills that are in addition to a core intelligence gift. The possession of absolute auditory pitch perception, for example, may be considered significant for musical ability but would be hardly considered an element of general intelligence (Rae & McAnulty, 1995; Zatorre, 2005). The fact that brain-imaging studies reveal different areas being activated by tasks associated with various cognitive abilities suggests that there may be different intelligences. Nevertheless, all of them may be modulated by variations in elementary neuronal functions that have to do with general intelligence (Houdé & Tzourio-Mazoyer, 2003; Murphy, 2003). Although the existence of several separate, modular intelligences instead of a single, molar intelligence has often been promoted (M. Anderson, 1998; Ceci, Nightingale, & Baker, 1993), this notion has just as often been denied (Chabris, 2007; Gerrans, 2002; Neubauer & Bucik, 1996; Petrill, 2002).

General Intelligence

Regardless of how one views it, there appears to be a general quality, conventionally called *g*, that is at the base of all human intellectual abilities (Detterman, 2000; Jensen, 2000). What is more, there are batteries of psychometric tests that measure it quite well. Note, however, that the tests are necessarily limited to tapping cognitive processes that can be demonstrated within a relatively short time span—that is, within the time frame of the tests. For example, it is typical to perceive a person's poor capacities in retaining episodic events over periods of a few days to several months as reflecting low intelligence. But it should be noted that the correlation between measures of earlier-occurring episodic events and standard intelligence test scores is rather weak (Alexander & Smales, 1997; about episodic memory in birds, cf. Clayton & Dickinson, 1998; Feeney, Roberts, & Sherry, 2009; Marzluff & Marzluff, 2011). Tests that would measure cognitive competencies over longer periods of time are plainly unwieldy.

Standard intelligence tests are specially designed to avoid the influence of special expertise, such as can be provided by relevant episodic or indeed procedural memories. Of course, there are also separate tests designed to measure the expertise that people like aircraft pilots or computer programmers may or may not have. A more interesting kind of test would be one that would measure the individual potential for the acquisition of any cognitive expertise rather than the actual possession of a particular expertise. This test would come close to the comparative assessment of the learning-to-learn capabilities of species described in the earlier section on animal intelligence. Note, however, that the capacity for higher-level learning in humans, if it were possible to reliably measure such a thing, would be unlikely to be totally divorced from short-term cognitive processing ability, the capacity that standard intelligence tests tend to assess.

Research into how people solve intelligence-test items, such as those shown in Figure 35.1, has revealed that they mainly challenge the working memory system (Baddeley, 1986; Logie & Della Sala, 2001; Oberauer, Süss, Wilhelm, & Wittmann, 2008). This mechanism apparently consists of two kinds of short-term memory: one dedicated to storing auditory-verbal (phonological) information and another dedicated to storing visuospatial information over time spans lasting several seconds to several minutes. Both of these stores have quite a limited capacity, as captured by the statement that they can hold no more than about 7 ± 2 chunks of information at a given time. The access to these buffers and the processing of their contents is controlled by a central executive mechanism. This agency is conceived as a serially operating device that is in some ways similar to the central processor of a computer. There is evidence that this working memory device plans and guides the course of our ongoing conscious behavior, but probably not the execution of more automated activities, the details of which we are largely unaware.

The neural networks that constitute working memory seem to be mainly located in the prefrontal cortex. In monkeys, lesions in this area impair the performance of tasks that require short-term information retention (Fuster, 1989). Moreover, electrophysiological recordings reveal neurons with response characteristics that are congruent with working memory functions (Funahashi & Kubota, 1994; Wallis, Anderson, & Miller, 2001). In humans, brain-imaging procedures consistently reveal that the prefrontal cortex is activated by mental tasks that resemble intelligence test items (D'Esposito et al., 1995; see also Koechlin, Basso, Pietrini, Panzer, & Grafman, 1999) and that it is more strongly activated by such items in lower-intelligence than in high-intelligence persons (Duncan, Burgess, & Emslie, 1995; but see Haier, Jung, Yeo, Head, & Alkire, 2004).

Intelligence tests can thus be thought to assess the information-processing capacity of working memory. Part of this quality seems to reside in the number of items that the audioverbal and visuospatial buffers can hold. Indeed, the so-called digit span—the average number of digits that an individual can reliably recall shortly after hearing or reading randomized lists of them—is a simple index known to appreciably correlate with the intelligence quotient (Schofield & Ashman, 1986; cf. Oberauer, Süß, Wilhelm, & Wittmann, 2008). But undoubtedly the relevant quality is also a function of the storage durability, the processing speed, the operational precision, and the computational complexity that the neuronal networks constituting the working memory system are capable of sustaining. At the species level, the fact that animals, pigeons more so than monkeys, have less capacious and less lasting short-term memories than humans might indeed be a reason why they are comparatively less intelligent (Wright, 1990; see also Higashijima, 2003; cf. Inoue & Mazusawa, 2007). How fast signals can be transmitted along axons and across synapses in the nervous system can be assessed at the individual level in humans by measuring the conduction velocity of polysynaptic pathways—for example, by recording the latency of cortical potentials evoked by peripheral stimuli (Reed & Jensen, 1993). Much like reaction times in multiple-choice tasks, where subjects must select a target stimulus among several distracter stimuli, these conduction velocities have been shown to partially correlate with their test intelligence. These two measures of neural performance have been found to be quite stable, lifelong traits of individuals, as long as no pathological events intervene (Neubauer, Spinath, Riemann, Borkenau, & Angleitner, 2000; Reed, Vernon, & Johnson, 2004; Walhovd et al., 2005).

Given the assumption that working memory for verbal and that for spatial information processing are somewhat independent, it may be that the effectiveness of the prefrontal cortex also depends on the processing capability of the several neural structures that provide it with inputs and outputs. Some of these accessory structures are undoubtedly functionally specialized networks supporting auditory, visual, verbal, manual, and other such functions, whose processing qualities may well surface behaviorally as one of the individually varying special abilities discussed earlier.

Is it possible that a high level of development of a particular modular ability could inhibit the expression of general intelligence? Excessive allocation of neuronal processing capacities to one sort of cognitive operation might restrict the capacities available for other kinds of cognitive functioning. The occurrence of so-called idiots savant suggests that there may be a competitive partitioning of computational resources (Heaton & Wallace, 2004; Hermelin, 2001; but see Snyder & Mitchell, 1999). Could it be that the above-average visuo-cognitive abilities of persons with the autistic Asperger syndrome are causally linked to their below-average social abilities (cf. Dawson, Soulières, Gernsbacher, & Mottron, 2007; Mayes & Calhoun, 2008)?

Developing Intelligence

Most of the studies that have examined concordances in intelligence quotients within pairs of monozygotic and dizygotic twins and between the intelligence quotients of adoptive children and that of their biological and adoptive parents have concluded that the ontogeny of intelligence is importantly, but not exclusively, determined by the individual's genome (Bouchard, 1993; Lyons et al., 2009; Plomin, De Fries, McClearn, & Rutter, 1997). This general conclusion is warranted despite the fact that the heritability of intelligence is an intricately complex issue (Grigorenko, 2000; Turkheimer, Haley, Waldron, D'Onofrio, & Gottesman, 2003). The undoubted role of the environment is still difficult to detail, largely because it is such a complex factor and because the effective environment is partly created by individuals themselves (Dickens & Flynn, 2001; Noble, McCandliss, & Farah, 2007; Scarr & McCartney, 1983). For instance, the availability of books at home is probably an intelligence-promoting factor, but of course, it can become effective only if the child is disposed to reading them.

The influence of the developmental environment on intelligence is possibly reflected in the fact that, over the decades since standardized intelligence tests have come into widespread use, the average intelligence of the population has been slowly but steadily rising, at least in developed countries (Neisser, 1998). This rise has occurred despite the fact that, in the same countries, there is a tendency for less intelligent couples to produce more offspring than more intelligent couples, a trend that should genetically depress the population's overall intelligence (Kirk et al., 2001; Lynn, 1999). The rise in average test intelligence seems to reflect improving standards of nutrition, health, and education. However, the rise might alternatively reflect increased outbreeding due to augmented mobility, which may counter the decline in intelligence that occurs in less mobile, inbred populations (Agrawal, Sinha, & Jensen, 1984).

Individual intelligence is also affected by birth order within the family, earlier-born siblings being at a slight statistical advantage over later-born siblings. This trend probably arises because intellectual nurturing diminishes in growing families—for example, baby babble increases and adult discussion decreases (Zajonc, 2001). However, the effect might also come about through a deleterious genetic aging of parental oocytes (and, less so, spermatocytes). Recall that Down syndrome (chromosome 21 trisomy) is more frequent in later-born children because of this aging (Carr, 1995).

Dire environmental events such as rubella infection during early pregnancy, protracted protein deprivation during childhood, or chronic lead poisoning during adulthood (Barth et al., 2002; Brown & Pollit, 1996; Zgorniaknowosielska, Zawilinska, & Szostek, 1996) can have a sizeable impact on the development and maintenance of test intelligence: More mundane environmental variants like bottle- or breast-feeding, maternal smoking or nonsmoking, and parental education levels have comparatively small impacts, but these and similar factors may interact and result in appreciable effects (Johnson, Swank, Baldwin, & McCormick, 1999; Neiss & Rowe, 2000; Rogan & Gladen, 1993; Wang et al., 2007). Even though intelligence quotients tend to be stable across the lifespan, the smaller fluctuations that nevertheless occur have been found to be related to subtle brain structure modifications (Ramsden et al., 2011).

One must keep in mind that the tens of thousands of structural and enzymatic proteins that make up the neurons of an individual are essentially products of the individual's genome present in each of these cells. Inasmuch as intelligence is importantly determined by the sophistication of neuronal network operations and these depend pivotally on the proteins that the genes can instruct, it has to be the case that the degree of intelligence that different species and different individuals exhibit must depend heavily on the genetic endowments that the species have come to possess and that the individuals have chanced to inherit. The decisive influence of genes on intelligence is illustrated, among other mutational defects, by the havoc that the fragile X chromosome mutant frequently wreaks in the intelligence of male and, more rarely, female persons (Dykens, Hodapp, & Leckman, 1994; see also Plomin, 2001; Skuse, 2005). Nevertheless, polymorphisms of a quite large number of genes, each of them having rather small effects, seem likely to be involved in the more common variations in intelligence (Deary et al., 2010).

Why it is that humans are overall so much more intelligent than chimpanzees—regardless of the fact that the latter may be superior in specific tasks (Inoue

& Matsuzawa, 2007)—when both species have about 99% of their almost 20,000 genes in common? The probable answer is that the several hundred genes that they do not share are crucially involved in regulating the expression of several thousand genes that determine brain development (Kaessmann & Pääbo, 2002; Levine & Tjian, 2003; Weissenbach, 2004). Both the proteinic composition and the anatomical structure of human brains are demonstrably more complex than those of chimpanzee brains (Enard et al., 2002; Holloway, 2001).

Epilogue

Even though, nowadays, test intelligence in many countries is no longer correlated with individual Darwinian fitness, as measured by the number of reproductively mature offspring produced, it still needs to be primarily understood as one of the many historical products of biological evolution. The cognitive competencies of some present-day animals unquestionably reflect some of the phylogenetic antecedents of human intelligent behavior. Tests that measure human intelligence yield scores that are characterized by a remarkable lifelong stability and a high genetic heritability. They assess the quality of neurobiological factors that determine the computational power of components of the brain that underlie problem solving through short-term reasoning. Longer-term learning and memory, capacities—more generally, longer-term cognitive flexibilities—that are part of more vernacular concepts of human intelligence (cf. Booth, 2002) and factors that are often central to animal intelligence assessments (cf. Fagott & Cook, 2006; Miyata & Fujita, 2008; Osvath, 2009), are not really measured by these tests.

Egalitarian-oriented people are frequently uncomfortable with the notion that intelligence is effectively, as suggested by E. G. Boring (1886–1968), defined by whatever the trait is that intelligence tests measures, and that what they measure is an individual disposition that is not easily improvable by a simple amelioration of the economic, educational, and social environment. They point out that test intelligence correlates only moderately with outward success in life (Mackintosh, 1998). It is indeed obvious that other traits, such as an intellectuality disposition (wanting to know) and an achievement motivation (wanting to succeed), also contribute to determining how well one does in life (Lloyd & Barenbatt, 1984). The assessment of their exact effects is hindered by the fact that these dispositions cannot be measured as precisely as can general intelligence. Furthermore, it seems that these partly heritable dispositions are somewhat correlated with general intelligence (Gagne & St. Père, 2002). The upshot is that test intelligence is still by far the best predictor of scholastic achievement and lifelong income that is available (Amelang, 1994; Schmidt & Hunter, 1998). But, one must note, it is clearly not at all a serviceable index of satisfaction with life (Pastuovic, Kolesaric, & Krizmanic, 1995; cf. Weiss, Bates, & Luciano, 2008).

The role of deliberative reasoning in intelligent behavior remains to be briefly considered. It is a process much involved in the solution of problems such as those presented in Figure 35.1. Humans can mostly state verbally, or pictorially, which analytical steps they undertook and what logical rules they applied when solving them (Carpenter et al., 1990). However, when examining the performance of humans on some tasks used to assess animal intelligence, one finds that many subjects cannot provide explicit after-the-event accounts (Siemann et al., 2004; Siemann & Delius, 1998). Moreover, those individuals who can provide explicit accounts do not as a rule exhibit any performance advantage. The solution of these tasks seems to rely on automatic processes that appear not to be fully consciously accessible. Phenomenologically, explicitly declarable, but usually covert, deliberative reasoning appears to correspond to a simulative neural operation that has similarities with overt trial-and-error learning. The learning takes place within an elaborate memorial representation (mental model) of the world and the self (cf. Churchland, 2002; Damasio, 2003; Ehrsson, Spence, & Passingham, 2004). This simulatory activity seems to rely heavily on a chess-playing-program–like mode of information processing: "Suppose I try this particular action, . . . no, it is not likely to lead to success, ... let's try this alternative action instead, . . . yes, this seems likely to work, . . . now I'll try this next step, . . ." and so on. Such deliberative reasoning may, in fact, often largely devolve in terms of corresponding sequences of visually imagined scenes (Knauff, Mulack, Kassubek, Salih, & Greenlee, 2002; Wohlschläger & Wohlschläger, 1998; cf. Neiworth & Rilling, 1987, about imagery in pigeons). Pictorial in-brain simulations of this kind are conceivably within the capabilities of clever animals such as corvids and might well underlie their "insightful" problem-solving feats (Bird & Emery, 2009; Heinrich, 2000; Prior, Schwarz, & Güntürkün, 2008). The evolution of language competence in humans, besides advancing a more clearly propositional style of covert deliberation (Fitch & Hauser, 2004;

Premack, 2004), might have also favored an increase in the informational definition and persistence of the mental representation. These modifications would have better allowed them to be semantically and syntactically explainable to others. Still, the continuing salience of the modeling imagery may possibly be what makes us feel that we, and perhaps others, our dogs included, are consciously aware of at least some of our thought processes (Griffin & Speck, 2004).

Acknowledgments

The present chapter is a much-modified and widely updated version of an earlier Spanish text (Delius, 2002). We thank I. Morgado-Bernal (Barcelona), M. J. Cleaveland (Poughkeepsie), S.-C. Li (Berlin), and J. M. Lee (Konstanz) for helpful comments and suggestions, and I. Straub (Konstanz) for pointing out relevant references. J. D. D. is grateful to the Deutsche Forschungsgemeinschaft, Bonn, for steady research support.

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