
IQ

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Introduction

Intelligence is the ability to think rationally, learn effectively, understand complex ideas, and adapt to the environment. Accordingly, intelligence is best seen as a general ability that can influence performance on a wide range of cognitive tasks. IQ (the intelligence quotient) is the quantification of an individual's intelligence relative to peers of a similar age. IQ is one of the most heritable psychological traits, and an individual's score on a modern IQ test is a good predictor of many life outcomes, including educational and career success, health, longevity, and even happiness (Gottfredson 1998). Like humans, several species of animals express a "general cognitive ability" that influences performance on broad and diverse cognitive tasks, and moreover, animals exhibit a wide range of individual variations in this ability.

Intelligence and Intelligence Testing (IQ) in Humans

It has long been recognized that intelligence varies across individuals. Colloquially, we refer to someone as "brilliant" or comment that our dog is a "little dull." While it is easy (and common) to

make these kind of characterizations, it has historically been difficult to formulate a definition of this trait. In 1995, a committee of the American Psychological Association stated that "Individuals differ from one another in their ability to understand complex ideas, to adapt effectively to the environment, to learn from experience, to engage in various forms of reasoning, to overcome obstacles by taking thought. Concepts of 'intelligence' are attempts to clarify and organize this complex set of phenomena" (Neisser et al. 1996). In an article in the Wall Street Journal (December 13, 1994) signed by 52 intelligence researchers, it was asserted that intelligence was "a very general mental capability that, among other things, involves the ability to reason, plan, solve problems, think abstractly, comprehend complex ideas, learn quickly and learn from experience. It reflects a broader and deeper capability for comprehending our surroundings."

The above definitions are simultaneously vague and broad. Although provided by experts on intelligence, they differ little (if only in form) from colloquial descriptions of the trait that one might hear from a random sample of college undergraduates. While it has been more than 100 years since Spearman (1904) formally described the concept of "general intelligence" (also called "g"), we still struggle with its definition, but nevertheless, we recognize it and we make inferences about its consequences. In this regard, the *quantification* of intelligence is best relegated to performance on psychometric tests.

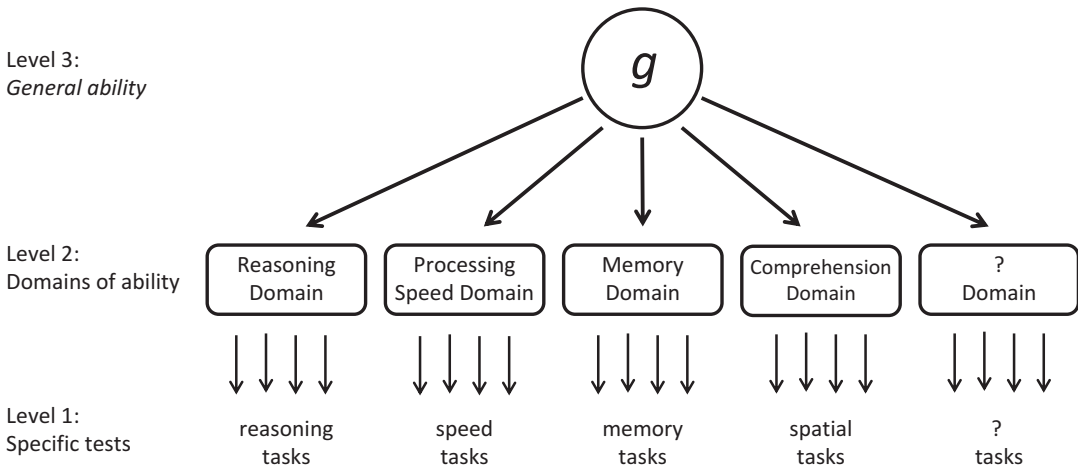
The rationale for most psychometric tests is roughly based on Spearman's early observation that performance on a wide range of cognitive tasks is positively correlated (i.e., if you perform well on one, you tend to perform well on others) and, as such, can be reduced to a single index of aggregate performance across a battery of diverse tests. In fact, psychometric tests (e.g., the Stanford-Binet, the Wechsler or WAIS, and the Raven's Progressive Matrixes or RPM) do differ in their content and structure. For instance, the Stanford-Binet includes questions that are culturally relevant and thus is best suited to predict performance in a particular culture's school system. The WAIS is less culturally biased but, like the Stanford-Binet, includes categories of questions that are presumed to reflect domains of abilities (verbal comprehension, working memory, perceptual reasoning, processing speed). An individual's performance on tests within a particular domain (e.g., reasoning) tends to be highly correlated, while performance on tests across domains (e.g., a reasoning task and a spatial task) is usually less correlated. Nevertheless, positive correlations are observed between performance on *all* tests in the battery. This is in line with the conclusion that *all* cognitive abilities are regulated (to varying degrees) by one general factor, or Spearman's "g," while other specific abilities might influence performance within a particular domain. These kinds of observations have led to the development of hierarchical models regarding the structure of intelligence, where *g* influences domains of specific abilities, which influence tasks within those domains. An illustration of a hierarchical model is provided in Fig. 1.

Since many studies on intelligence use factors analyses, a brief explanation of this technique is warranted. Briefly, a factor analysis is a statistical method which reduces a large number of correlations into as few explanatory factors as possible. If, for example, all of the correlations across several tests of cognitive ability are strongly positive, the factor analysis recognizes that a common source of variance contributed to performance on all tasks, and this would be described as a general factor. In reality, the outcome of such an analysis can be much more complicated, and of course we

might be interested in large numbers of cognitive tasks, some of which represent clusters of what are presumed to be specialized abilities. In these cases, the factor analysis might extract a general factor, as well as secondary factors, which explain relationships between only subsets of the tasks being considered. Of course, if no single source of variance was common to all tasks, a factor analysis might reveal no common factor at all. When factor analyses are performed on human intelligence test data (such as from the WAIS), it is typical to find a general factor (i.e., general intelligence) as well as secondary factors that describe specific cognitive domains (e.g., spatial abilities; see Fig. 1).

Remember that the Stanford-Binet and the WAIS include tests of many different abilities, and an individual's aggregate performance across all of these tests is used to estimate that individual's intelligence. In contrast, the RPM is an intelligence test that is based exclusively on only *one* ability and, accordingly, includes only progressively difficult tests of perceptual (analogical) reasoning. This test structure is based on an assumption that reasoning is representative of *the* core ability that regulates all intelligence (Raven et al. 1998). Because of its format, the RPM requires no knowledge of culture or language.

Unlike a qualitative description of intelligence, the IQ *score* is a *quotient*, that is, it is an individual's score on a standardized test *relative* to that individual's age-matched peers. It is true that an individual's IQ score will tend to remain stable across the lifespan, i.e., the IQ scores of a group of 8-year-olds will be highly correlated with their scores at 90 years of age ($r = \sim .80$). This does *not* mean that individual's raw cognitive ability is the same across the lifespan. For example, were we to administer an RPM to one individual at 8, 25, 50, and 90 years of age, the number of correct answers would be about the same at 8 and 90 years of age, while at 25, the individual would answer at least twice as many questions correctly (with the 50-year-old somewhere in between). So why do we say that an individual's IQ remains constant across the lifespan? Because IQ is approximately unchanging *relative* to persons of a similar age,



IQ, Fig. 1 The hierarchical model of intelligence. *Level 1* represents specific tests that are emblematic of various domains of cognitive ability. Some potential domains are illustrated in *Level 2*. The number and content of these domains is a matter of some debate, although there is wide agreement on the existence of the four domains that are illustrated. The fifth domain (?) acknowledges that other domains may exist. People who perform well on tasks from

one domain tend to perform well on tasks from other domains. This suggests the existence of a general influence on cognitive abilities, represented in *Level 3*. This general influence is commonly referred to as general intelligence or simply “intelligence.” This model does not require only *one* type of intelligence. Rather, it assumes that a general ability influence other more domain-specific abilities.

i.e., a person who is smarter than most of his/her peers at 8 years of age will be smarter than his/her peers at 50 and 90 years of age (Deary 2014), despite the inevitable truth that our cognitive abilities decline with age.

Regarding the nature of intelligence or IQ, many persons will incorrectly assume that high intelligence is necessarily reflected in a high level of *knowledge*. In fact, high intelligence promotes the ease with which we acquire knowledge, but intelligence itself is independent of knowledge. Why then do some IQ tests (such as the Stanford-Binet) have components that test knowledge? Simply because all other things being equal, a smarter individual is likely to acquire more knowledge. Learning is *easier* for that individual than it might be to someone of lesser intelligence. In this regard, scholastic aptitude tests such as the SAT are often a good approximation of intelligence as measured on a knowledge-free test such as the RPM ($r = .5-.6$). However, knowledge and intelligence need not always be related. For instance, an individual with innately high intelligence might (through some act of fate) live in an impoverished environment where the

opportunities to acquire knowledge are severely limited. This is exactly why an IQ test such as the RPM has no measures of knowledge (only perceptual reasoning) and is considered by many to be a more pure measure of innate ability.

Given the different content and structure of psychometric intelligence tests, it might be surprising to find that individuals’ scores on these tests are strongly correlated (r s will typically range from 0.8 to 0.9). Even more surprising is the popular assertion (sometimes even by some with advanced degrees in psychology) that “IQ tests measure nothing of functional significance.” Standardized intelligence tests first received widespread recognition owing to the US government’s use of a modified version of the early Stanford-Binet to determine assignments of new recruits in World War I. These assignments were highly effective (relative to the previous practice of assignments based on patronage or chance) and are widely regarded as having contributed to the USA’s success in WWI. Since that time, we have collected a wide array of data regarding the predictive capacity of IQ tests. For instance, a child’s IQ score is highly predictive of obvious outcomes

such as educational and career success, as well as lifetime income. But IQ test performance predicts many less obvious outcomes such as the distance one will travel from his/her place of birth, the likelihood of incarceration, the likelihood of drug addiction, the age of death, incidence of type II diabetes, ratings of happiness, and even your *spouse's* income and IQ (for a comprehensive review of the predictive capacity of the IQ test, see Gottfredson 1998). IQ scores are even inversely related to the likelihood that an individual will murder their spouse! To quote Gottfredson (1998, page 24), “No matter their form or content, tests of mental skills invariably point to the existence of a global factor that permeates all aspects of cognition. This factor seems to have considerable influence on a person’s practical quality of life. Intelligence as measured by IQ tests is the single most effective predictor known of individual performance at school and on the job” as well as many other aspects of well-being. Thus, far from being a “social construct” with no functional significance, the modern IQ test is a highly effective (and widely used) diagnostic and predictive tool.

Intelligence in Nonhuman Animals

Although studies of individual differences in animal intelligence had been frequent early in the twentieth century (Thorndike 1911, 1935; Tolman 1924; Tryon 1940), the emergent focus on experimental (rather than correlational) studies tended to limit the interest in this topic in the later part of that century. However, during the past two decades, interest in individual differences in animal intelligence has seen a dramatic reemergence. As discussed above, contemporary definitions of intelligence tend to be vague, broad, and, to some degree, a matter of debate (Sternberg 1985). Nevertheless, psychometric tests of intelligence do appear to characterize a trait captured in both colloquial and empirical definitions of intelligence, i.e., the ability to understand, learn, and reason. To explore a trait analogous to intelligence in nonhuman animals, researchers have developed tests to characterize a similar set of skills, most notably in mice and monkeys.

Genetically heterogeneous mice (i.e., mice with genetic variability that translates into measurable individual differences) have been tested on large batteries of cognitive tasks to determine the existence of a general cognitive ability in mice analogous to IQ. In one such study (Kolata et al. 2008), 241 mice were tested on seven cognitive tasks, which included tests of working memory capacity, associative learning, operant learning, and spatial learning abilities. Using factor analysis, it was observed that a general factor influenced performance in these mice and this factor accounted for 38% of the variance across tasks. This is comparable to what is known from tests of humans’ abilities, where it is believed that general intelligence accounts for 40–50% of the variance in performance across a broad array of cognitive tests. In addition, a domain-specific factor was found to account for the performance of mice on a subset of tasks that shared a dependence on spatial processing. These results provide evidence for a general learning/cognitive factor in genetically heterogeneous mice. Furthermore (and similar to human cognitive performance), these results suggest a hierarchical structure (see Fig. 1) of cognitive abilities in mice, where a general factor influences performance on subdomains of abilities. Importantly, mice also exhibited considerable variability in their general cognitive performance. In fact, the general abilities of mice were normally distributed, such that most mice expressed average abilities, while some were “bright” (performing well on all tasks), while some were “dull” (performing poorly on all tasks).

As described above, reasoning is considered to be a hallmark of intelligence and is considered by some to be *the* general factor that underlies variations in intelligence. It has previously been established that humans are capable of “fast mapping” (Carey and Bartlett 1978), a process whereby a new concept can be acquired based on a logical inference, corresponding with Aristotle’s description of deductive reasoning. Fast mapping is believed to play a critical role in the extraordinarily rapid acquisition of information during early human development and explains (in part) the prodigious rate at which children gain vocabulary. For

example, when faced with a group of familiar items described by familiar words, an infant will quickly associate an unfamiliar word with a novel item added to the set of familiar items, and this association requires no overt “pairing” of the novel word and its corresponding novel item.

Fast mapping based on responses to human language has also been demonstrated in dogs (Tomasello and Kaminski 2004; Pilley and Reid 2011), where border collies can successfully find a novel object when commanded (with a novel word) to retrieve that novel object from within a large set of familiar objects. Using a similar strategy, fast mapping has been assessed in mice, although the task was not based on responses to language. Mice were first trained to associate pairs of objects, where, upon exposure to a sample object, the correct choice of a target object earned the mouse a food reward. Following training, the mice could successfully use the sample object to guide its choice of a target object out of a set of familiar objects. (This type of performance is emblematic of “paired associate learning.”) To test “fast mapping,” the animal was then presented with a novel sample object and allowed to choose a target object from a set containing several familiar objects and one novel object. If the mice were capable of fast mapping (inference by exclusion), they should choose the novel target object (in response to the novel sample) since all other objects in the set had a previously established meaning. Mice perform quite well in this task, choosing the novel object at an average rate far better than chance. However, not all mice perform similarly, and while some exhibit perfect performance, some consistently make incorrect choices. The likelihood of a mouse’s success in this fast mapping task is correlated with their performance on other more elemental cognitive tasks (e.g., associative learning, spatial learning, operant learning), suggesting that as in humans, this form of reasoning ability is related to more general cognitive abilities (Wass et al. 2012).

General cognitive abilities of mice have also been described by Galsworthy et al. (2002), who compared the performance of 40 genetically heterogeneous mice across a battery of cognitive tests distinct from those reported in the studies

described above. All measures of cognitive performance loaded positively on a principal component that accounted for 31% of the variance across mice, again suggesting the presence of a common influence on performance on all tasks. In addition, Galsworthy et al. calculated the heritability of this general cognitive ability in mice. (This was accomplished through a classic sibling analysis, which assesses the degree of relatedness between siblings on some variable of interest, in this case general cognitive ability.) The heritability of the general cognitive ability of mice was estimated at approximately 0.4 (on a scale of 0–1), suggesting a moderate genetic contribution to the expression of this trait. These results of Galsworthy et al. are quite informative. They indicate that the “intelligence” of mice is moderately heritable, at a level that is comparable to what is observed among teenage humans. Note that the heritability of human intelligence actually *increases* across the lifespan, reaching a plateau of approximately .80 at 50 years of age. This increase in heritability is presumed to reflect the interactions of genes with the environment, where persons of similar IQ become even *more* similar as they gravitate to similar cognitive challenges. Unlike typical humans, laboratory mice are maintained in a behaviorally sterile and homogeneous environment. Consequently, these mice cannot select the environments or challenges that might maximize cognitive differences, thus constraining the gene-environment interaction.

In addition to rodents, individual differences in a general cognitive ability have been observed in several species of nonhuman primates. While most studies of nonhuman primates have been designed to compare differences in intelligence between species (leading to a popular hypothesis that brain size is related to intelligence; Burkart et al. 2016), at least one study was designed explicitly to assess individual differences in the expression of a general cognitive influence within a single species. Banerjee et al. (2009) administered a large and diverse battery of cognitive tests to 22 tamarin monkeys (*Saguinus oedipus*). The cognitive tasks covered a wide range of cognitive skills and domains, including occluded reach, targeted reach (reward retrieval from a moving

pendulum), adaptation to an observed change in reward location (a measure of executive control), reversal learning, novel object recognition, numerical discrimination, acoustic habituation, object tracking (an index of attention), social tracking (gaze at a conspecific), hidden reward retrieval after various delays, and a food retrieval puzzle (which was asserted to tax reasoning). Banerjee et al. observed positive correlations in the monkeys' performance across all tasks. Using a type of factor analysis, all tasks loaded positively on a common factor. The weight of these loadings (an index of the degree to which a variable is impacted by that factor) could be described as "weak" to "moderate." Expectedly, the tasks with the least obvious cognitive demands (targeted reach and social tracking) loaded most weakly. In total, these results provide evidence for individual differences in the expression of a general cognitive ability among tamarins, and moreover, that the general factor's influence is directly related to the level of the cognitive demand.

What is the Latent Factor that Regulates Intelligence?

Many factors, such as speed of processing or brain size, have been suggested to underlie variations in intelligence. However, correlational analyses have typically found only weak relationships between these factors and intelligence. Two clear exceptions should be noted. Both reasoning ability and working memory capacity are strongly predictive of IQ (and as noted previously, the RPM intelligence test is based solely on performance on analogical reasoning tasks). Although it was once commonly asserted that reasoning ability was *the* latent factor which regulated individual differences in intelligence, it has been more recently hypothesized that working memory may serve such a function. In his classic textbook on intelligence, Mackintosh describes the full rationale for this hypothesis and points out that it is easy to surmise the way that working memory could influence reasoning, as will be seen below, while it is more difficult to imagine the opposite being true (Mackintosh 1998).

Since their inception, intelligence test batteries commonly included tests of simple memory span

(e.g., the number of items from a briefly studied list that an individual can correctly recall). Somewhat surprisingly though, this seemingly elemental ability has only a weak relationship to general intelligence. In 1980, an important observation by Daneman and Carpenter (1980) shed light on the relationship between memory and intelligence. Daneman and Carpenter found that simply remembering a list of words was only weakly related to general intelligence (in this case, estimated through reading comprehension). In contrast, if the same words appeared at the end of sentences, the ability to remember those words was strongly correlated with general intelligence. This led to the hypothesis that simple retention had only a small (if any) role in the regulation of intelligence, while "working memory capacity" had a more central role.

While short-term memory simply holds information, the working memory system is one which stores information while manipulating and utilizing that information (often during conditions of high interference) for a particular goal. Working memory is employed for most cognitive tasks. For instance, your ability to read and comprehend this paragraph requires that you remember words, synthesize the meaning of strings of words, and try to extract the overall message embedded in those strings of words. Obviously, your memory and manipulation of words and thoughts can become confused depending on the content of the paragraph. A similar rationale for the implementation of working memory can be applied to virtually any task; imagine doing a mental math problem or solving a spatial puzzle. In this regard, an analogical reasoning problem (such as might appear on the RPM test of intelligence) requires the individual to hold potential solutions in memory, compare the utility of those solutions, revise the solutions, and store the revised solutions in temporary memory. But while analogical reasoning depends on the efficient application of working memory, it is not clear that the application of working memory has any dependence on reasoning abilities. It is this ubiquitous demand for working memory that has led to the assertion that working memory may be the basis for the overall performance on an intelligence test.

Since the original report of Daneman and Carpenter, many studies have found evidence for the relationship of working memory capacity to general intelligence (for a brief review, see Engle 2002).

Unlike human research, only limited work has been done to assess the relationship between working memory and intelligence in nonhuman animals. Some studies have found a relationship between working memory and intelligence in mice, but such correlations cannot be assumed to reflect a cause-and-effect relationship. The direction of cause between working memory and intelligence cannot be determined, and moreover, both traits might be influenced by a third, hidden variable. It should be noted that the same difficulties exist when interpreting this relationship in humans. However, in both humans and mice, a causal relationship between working memory and intelligence has been explored. For instance, Jaeggi et al. (2008) exposed humans to intensive working memory training by having them perform a “dual n-back” task for several weeks. The dual n-back task requires the subject to simultaneously monitor a stream of visual and auditory cues (a sequence of visual locations and a sequence of auditory letters). The subject’s task is to identify matches that occur in each stream of information (e.g., auditory “B” matches auditory “B,” or upper right grid location matches upper right grid location) that occur a specific number of places back in the stream of information, e.g., 2-back, 3-back, and 4-back. Humans typically find this task to be extremely difficult (and even stressful), and the larger the n-back requirement (e.g., 4-back rather than 2-back), the more difficult the task becomes. This task is considered to tax working memory capacity, and humans will typically improve across days of training; they may initially find 2-back to be *very* difficult but might eventually master 6-back. Jaeggi et al. observed that several weeks of such training improved working memory and had positive (although small) effects on intelligence test performance. This suggests that working memory has a direct *causal* influence on an individual’s intelligence.

The work by Jaeggi et al. (2008) is by no means conclusive. While it has been replicated several times, others have failed to replicate these results, often after extensive attempts to do so (Redick et al. 2012; Shipstead et al. 2012). Relatedly, commercial “brain training” devices based on working memory training have been widely criticized as ineffective (Simons et al. 2016). Although this controversy has not been resolved, it is clear that training working memory in humans is complicated by the fact that humans *regularly* engage in the use of working memory outside of the laboratory (e.g., your comprehension of this paragraph), and so any working memory training that occurs in the laboratory is small in comparison. To this end, it might be useful to consider the effects of working memory training on laboratory animals that live in sterile cognitive environments. Light et al. (2010) developed a task to train working memory in mice. In this task, the mice were required to perform simultaneously in two mazes, and each maze required the animals to keep track of eight locations. Since the locations were marked by a common set of visual cues, the mice become very confused (presumably owing to an overload of working memory). Like n-back training, mice get better at these mazes over a period of weeks and, when later tested, exhibit improvements in working memory. Likewise, they exhibit improvements in general cognitive performance, suggesting that the efficacy of working memory can under certain circumstances have a direct causal impact on a mouse’s intelligence. In the case of both humans and mice, these studies of the impact of working memory training on intelligence provide further evidence that intelligence is *malleable*. That is, although intelligence is heritable, genes interact with environmental experience to regulate an individual’s IQ.

Space does not permit a detailed explanation of the neuroanatomical systems that contribute to the expression of intelligence or working memory. However, these kinds of analyses also suggest that these abilities are strongly related. Brain areas that are active during tests of general intelligence overlap considerably with brain areas active during performance of a working memory task (Jung and Haier 2007), and the same brain

areas have been implicated in the processing of working memory in both monkeys (Konecky et al. 2017; Riley and Constantinidis 2015) and rodents (Wass et al. 2013). In total, and although this issue is far from resolved, our current state of understanding suggests that variations in working memory capacity contribute directly (at least in part) to variations in intelligence.

Conclusion

Humans and nonhuman animals exhibit individual differences in their ability to “reason, plan, solve problems, think abstractly, comprehend complex ideas, learn quickly and learn from experience” (Neisser et al. 1996). This complex of abilities is referred to as intelligence. In both humans and animals, this trait can be assessed through batteries of cognitive tests, and in humans, these tests give rise to an intelligence quotient (an “IQ score”) which quantifies an individual’s performance *relative* to those of a similar age. Studies in nonhuman animals, most remarkably in primates and mice, have utilized diverse batteries of cognitive tests to measure something analogous to IQ. The intelligence in these animals varies among individuals and seems to be correlated with processes such as reasoning and working memory. Recent research in both humans and mice suggest that working memory training might make causal contributions to the improvement of IQ. Those findings have not only theoretical implications concerning the structure and neurobiological insatiation of intelligence, but it also opens up opportunities for future practical applications.

Cross-References

- ▶ Analogical Reasoning
- ▶ Behavioral Genetics
- ▶ Behavioral Variation
- ▶ Brain Size
- ▶ Deductive Reasoning
- ▶ Genetic Variation
- ▶ Heredity

- ▶ Heritability of Behavior
- ▶ Inductive Reasoning
- ▶ Intelligence
- ▶ Learning
- ▶ Raven Scales
- ▶ Working Memory

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