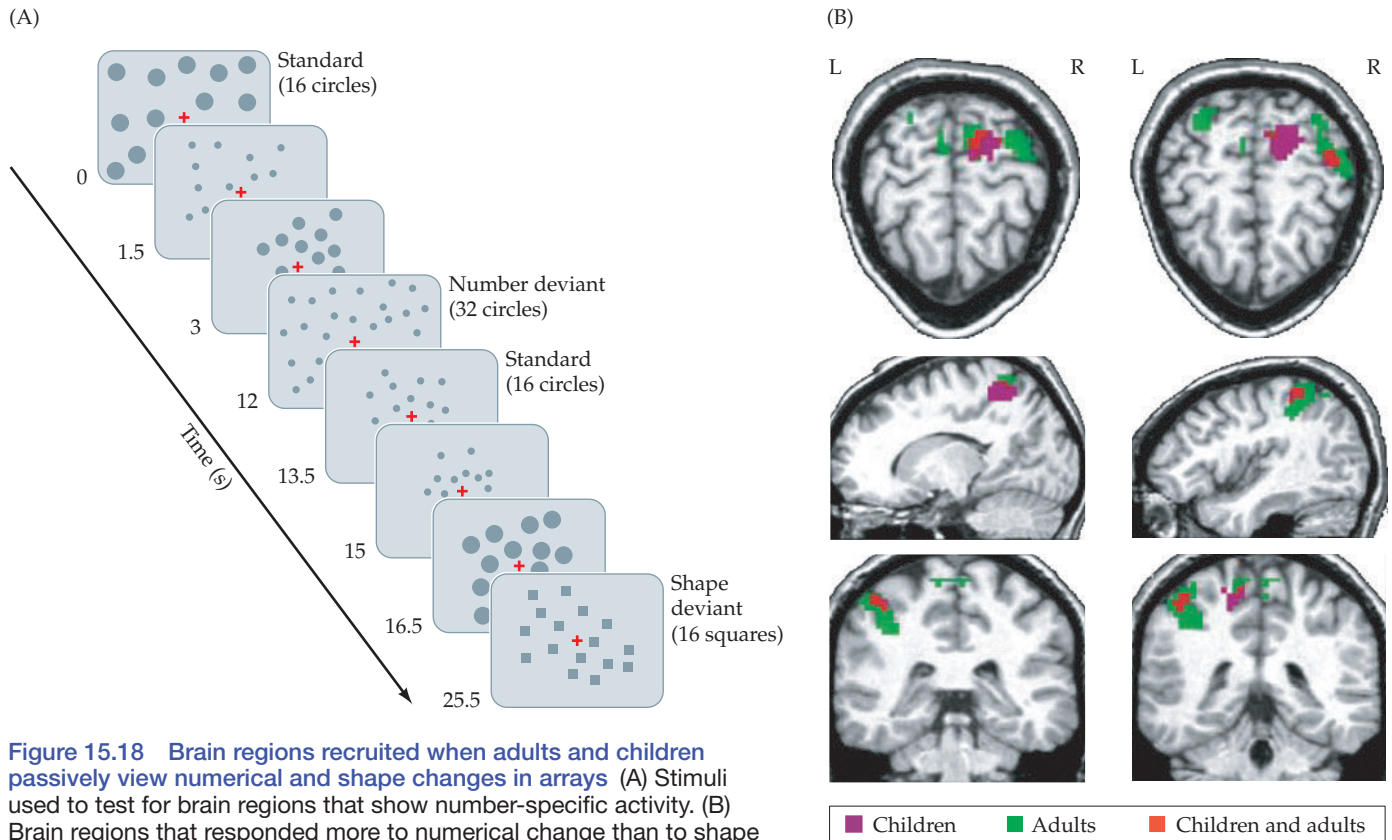




the same brain region appears to be recruited when infants and very young children perform numerical tasks. For example, a study with infants using near-infrared spectroscopy (NIRS) showed that the IPS in the right hemisphere responds selectively to changes in the number of elements compared to changes in shape of a visual stimulus. Similarly, both 4-year-old children and adults show selective recovery of fMRI BOLD responses to changes in the number of stimuli but not changes in the shape of stimuli within the same IPS region (Figure 15.18). In rhesus macaques, cells in the prefrontal and parietal cortices respond selectively to specific numerical values (Figure 15.19). The sensitivity of individual neurons to number is broader for larger numbers, consistent with encoding number on a ratio scale.

Collectively, these findings strongly implicate the IPS as a critical component, if not the physical embodiment, of the ANS. One implication of this conclusion is that the ubiquitous problem of quantifying things in the world selectively favored the evolution of a homologous brain circuit supporting approximate number judgments early in primate evolution, and this circuit is operational early in human infancy. These ideas raise the question of how the brains of other animals, as diverse as birds, bees, and spiders, make numerical judgments in a way similar to those made by the ANS in monkeys and humans.

Evolution and development of social cognition

Most primates, including humans, live in relatively large social groups structured around kinship, dominance hierarchies, and cooperative alliances. Managing these social relationships relies on individual recognition, status assessment,

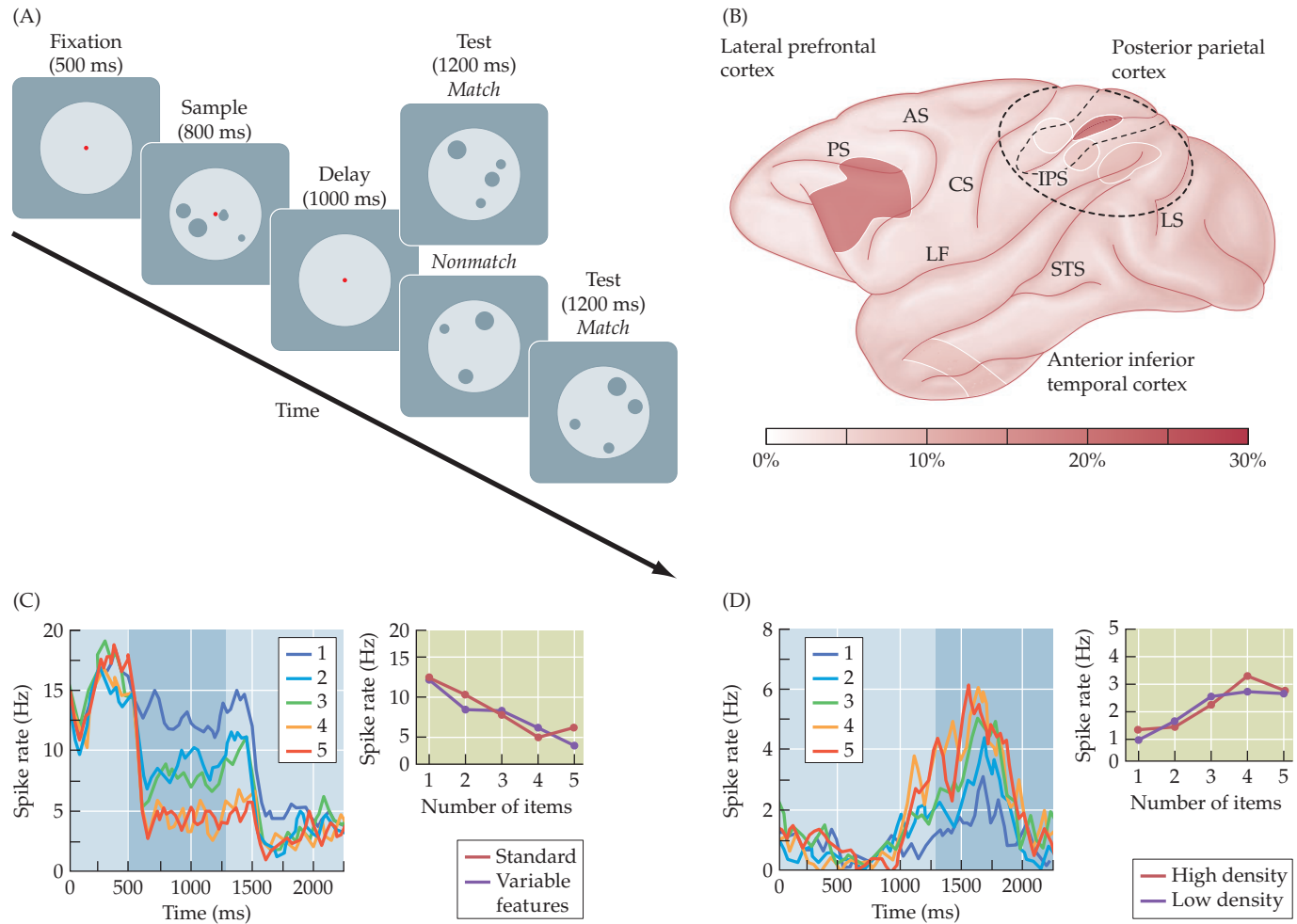


Figure 15.19 Evidence for number cells in the parietal cortex of the monkey brain (A) Stimuli like these were used in the task structure illustrated here to test macaques during electrophysiological recording. Monkeys viewed sample arrays and after a short delay were required to release a bar when the test array matched the sample array in number. (B) This lateral view of a monkey brain shows recording sites. Color coding indicates the relative proportion of number-selective cells. AS, arcuate sulcus; CS, central sulcus; IPS, intra-parietal sulcus; LF, lateral fissure; LS, lunate sulcus; PS, principal sulcus; STS, superior temporal sulcus. (C) Firing rate is plotted as a function of sample numerosity during the sample period (darker shaded region) for a neuron that was maximally responsive to one item, the numeral 1. (D) Here, firing rate is plotted as a function of sample numerosity during the delay period (darker shaded region) for a neuron that was maximally responsive to four items. (After Nieder and Miller 2004.)

and long-term memory for prior interactions. Furthermore, it would be adaptive for primates to be able to infer the intentions of other individuals from their expressions and state of attention, as well as to be able to deceive others. Such socially sophisticated behavior implies an ability to infer the internal mental state of other individuals (see Chapter 11). This hypothesis of socially driven brain evolution is often referred to as the *Machiavellian intelligence hypothesis*, after the notorious political theorist of the Italian Renaissance.

The suggestion that the more highly evolved cognitive abilities of primates in general and humans in particular have been socially driven is supported by several observations. First, primate societies are arguably among the most complex in the animal kingdom, and primates as a group possess relatively large forebrains. Moreover, other animals that live in complex social groups, such as dolphins and killer whales, also have relatively large brains. Second, various measures of advanced brain development among primates correlate with measures of social complexity such as deception rate, number of grooming partners, and frequency of social learning and innovation (Figure 15.20). Third, the primate brain also shows specializations for processing social information. Both human and non-human primates, for example, possess neurons in the temporal and occipital cortex selective for the identity and direction of gaze in a viewed face (Figure 15.21A; see also Figure 3.27A). Moreover, electrical stimulation of areas containing such face-selective neurons in monkeys can induce them to report seeing a face; stimulation of the temporal cortex and

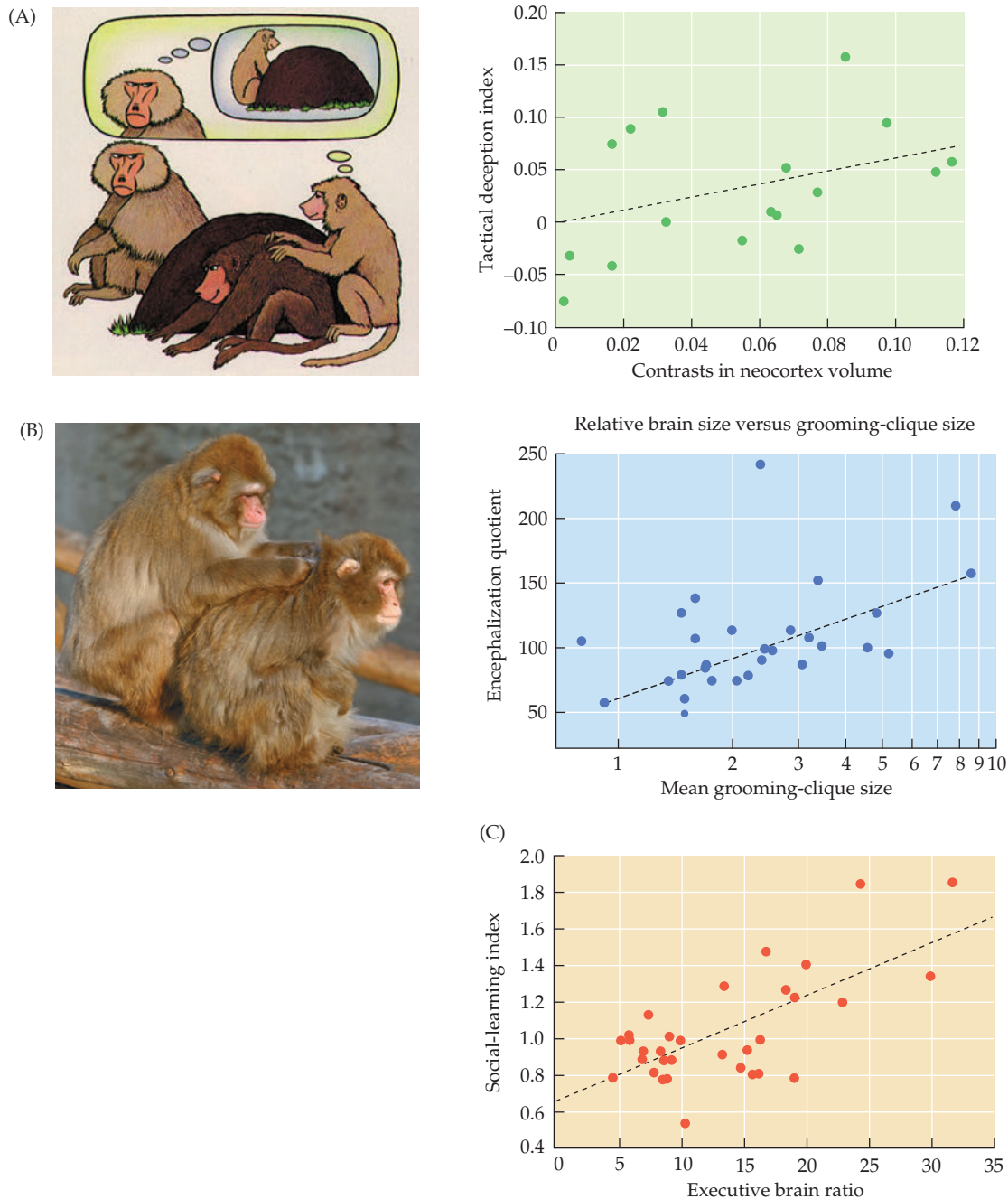


Figure 15.20 The social, or Machiavellian, intelligence hypothesis Most primates live in groups that favor the evolution of sophisticated social skills, including the ability to infer the emotions and intentions of others. Such skills would favor the evolution of advanced cognition in primates. (A) The sort of tactical deceptive abilities illustrated in the cartoon on the left tend to be greater in primates with larger neocortices. (B) Encephalization quotient, a measure of brain size to body size, scales positively with grooming-clique size, which is the typical number of animals that an individual spends time grooming. (C) Social-learning frequency scales positively with executive brain ratio, a measure of the elaboration of advanced brain structures, including the prefrontal cortex. (A after Byrne and Corp 2004; B after Kudo and Dunbar 2001; C after Reader and Laland 2002.)

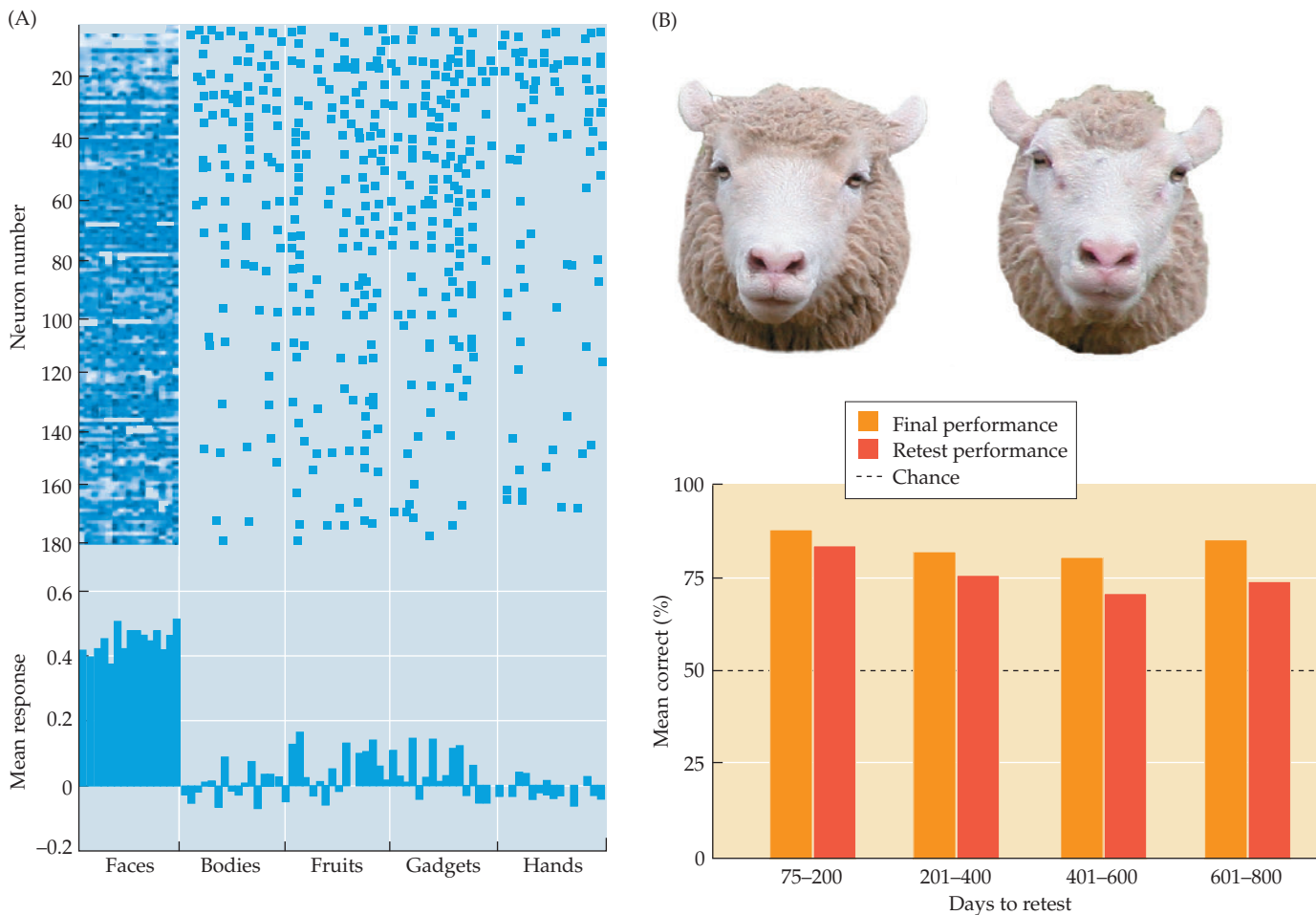


Figure 15.21 Social recognition (A) Neurons in a face “patch” in the monkey temporal lobe identified by fMRI respond selectively to faces. Each tick (upper portion of panel) marks neuronal firing to a stimulus by the individual neurons displayed in each row in the graph. Average responses across all neurons were robust for faces but weak for other complex objects (lower portion of panel). (B) Sheep can remember the faces of their cohorts for up to 3 years. (A after Tsao et al. 2006; B after Kendrick et al. 2001.)

fusiform gyrus can induce transient prosopagnosia—a specific deficit in face recognition (see Chapter 3) in human surgical patients. Such specializations are not unique to primates, however; sheep have similar face-selective neurons in their temporal cortices and, despite their simple social system, are adept at recognizing and remembering social identities (**Figure 15.21B**).

Remarkably, the neural circuits implicated in identifying individuals, attending to the face and body cues that communicate their intentions, and acting on this information not only are well developed in human and non-human primates but are shaped by social conditions even during adulthood. A recent study experimentally manipulated group size, from one to six individuals, in a colony of rhesus macaques. The monkeys’ brains were subsequently scanned while they were anesthetized. Structural MRI scans showed that the gray matter in the superior temporal sulcus region of cortex—an area known to contain neurons selective for faces—was thicker in monkeys with larger social networks (**Figure 15.22**). Furthermore, there was stronger functional coupling between this region and a region of prefrontal cortex implicated in planning and decision making. Finally, these relationships were more pronounced in monkeys with higher status.

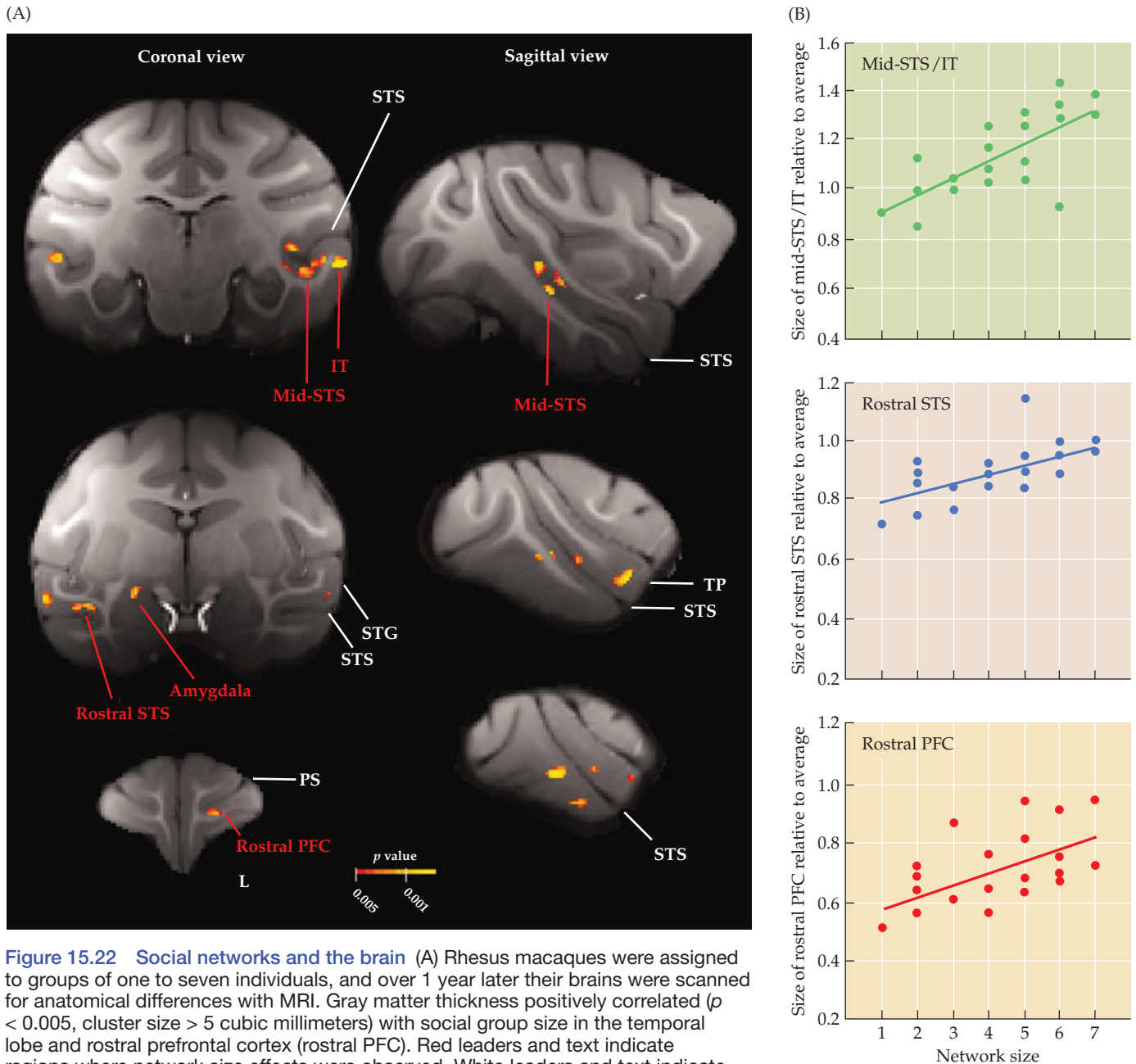


Figure 15.22 Social networks and the brain (A) Rhesus macaques were assigned to groups of one to seven individuals, and over 1 year later their brains were scanned for anatomical differences with MRI. Gray matter thickness positively correlated ($p < 0.005$, cluster size > 5 cubic millimeters) with social group size in the temporal lobe and rostral prefrontal cortex (rostral PFC). Red leaders and text indicate regions where network size effects were observed. White leaders and text indicate anatomical landmarks. IT, inferotemporal cortex; L, left; PS, principal sulcus; STG, superior temporal gyrus; STS, superior temporal sulcus; TP, temporal pole. (B) The relationship between social network size and a measure of the size of the mid-STS/IT, rostral STS, and rostral PFC, relative to the overall average. Measures greater than 1 indicate that voxels in an individual's MRI scan must be compressed to match the group average. (After Sallet et al. 2011.)

Together, these observations endorse the idea that individual experience can shape the structure and function of neural circuits supporting specialized types of cognition, and they hint at the remarkably interplay of development, experience, and evolution in adapting individuals and species to specific information-processing problems presented by the physical or social environment.

Supporting the importance of social interaction in the evolution of human cognition, developmental studies suggest that specializations for processing

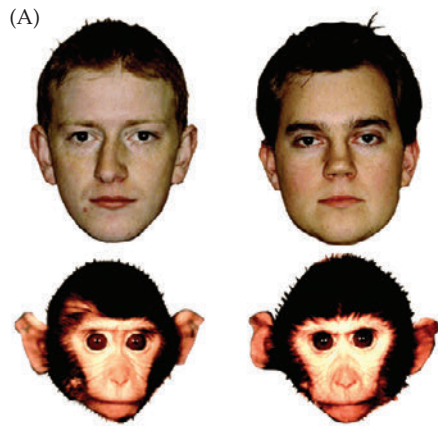
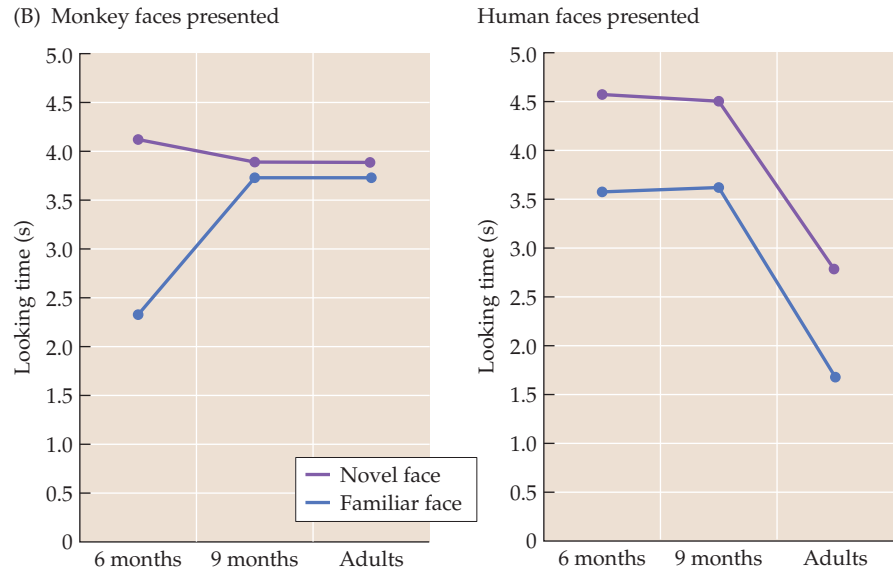


Figure 15.23 The “own species” effect (A) Sample stimuli. (B) Six-month-old infants show longer looking times when presented with both novel monkey (left graph) and human (right graph) faces. In contrast, 9-month old infants (and adults) differentiate novel faces from familiar faces only in humans. (After Pascalis et al. 2002.)



social information appear early in human ontogeny and become refined with the development of social expertise, and that their dysfunction in conditions like autism can have devastating consequences. Infants enter the world with a bias to attend to faces, and even in the first few months of life they differentiate novel individuals from each other. Much like adults, infants only a few days old show superior discrimination for upright faces compared to inverted faces. Further, the P100 and P400 ERPs recorded from 3-month-old infants differentiate upright and inverted faces as well.

Building on this initial face-processing bias, face perception in infancy is also shaped by experience. For example, 6-month-old infants show similar recognition memory for both monkey faces and human faces. By 9 months, however, infants, like adults, are better able to recognize human faces compared to monkey faces (Figure 15.23). Increasing specialization for own-species faces mirrors the phenomenon of perceptual narrowing seen in speech perception, in which infants initially perceive phonemes of all languages but gradually lose the ability to perceive phonemes not present in the language they are exposed to (see Chapter 12).

As might be expected, given the highly social nature of our species, failure to develop normal social cognition can have devastating consequences. Autism, for example, is a disorder that affects about three to six in every 1,000 children and, as described in Chapter 11, involves many social deficits. Individuals with autism tend to avoid both physical and eye contact with others. They show heightened interest in the inanimate world, often fixating on particular objects. In addition, children with autism tend to fail theory-of-mind tasks and generally show reduced interest in other people. In contrast to typically developing children and adults, people with autism spend significantly less time examining people’s eyes and instead focus on the mouth or body when shown images of people.

By contrast, children with Williams syndrome—a neurodevelopmental disorder characterized by high verbal abilities but otherwise low IQ and excessive sociability—show relatively normal social cognition, orienting to faces and successfully passing theory-of-mind tests. The contrast between children with Williams syndrome, who are typically social and talkative, and children with autism, who are typically antisocial and reticent, has been interpreted by some as evidence that social cognition depends on a dedicated brain system that

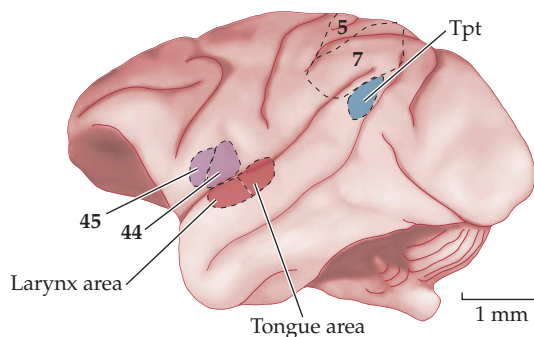
can be disturbed during development. However, research by developmental psychologist Annette Karmiloff-Smith and her colleagues suggests some caution in the interpretation of this contrast. For example, children with Down syndrome show impaired face processing but nonetheless pass theory-of-mind tests. Karmiloff-Smith argues that segregation of social cognition may occur postnatally, through experience with normal social and speech input. In any event, developmental disorders of this sort are clearly complicated and are more likely to depend on a cascade of developmental events that has gone awry than on the loss of a specific regional function.

Evolution and development of language

As introduced in Chapter 12, two brain regions in the left hemisphere appear to be major substrates for language processing in humans. Broca's area in the frontal cortex plays a critical role in language production, and lesions in this area produce an aphasia characterized by halting, inarticulate speech. Wernicke's area in the temporal lobe contributes to language comprehension, and lesions in this area result in deficits in producing meaningful utterances.

Although it was initially thought that Broca's and Wernicke's areas were unique to humans, it now appears that they represent elaborations of brain areas present in non-human primates (**Figure 15.24**). Field playback experiments of species-specific vocalizations in macaques have shown a right-ear

(A) Macaque



(B) Human

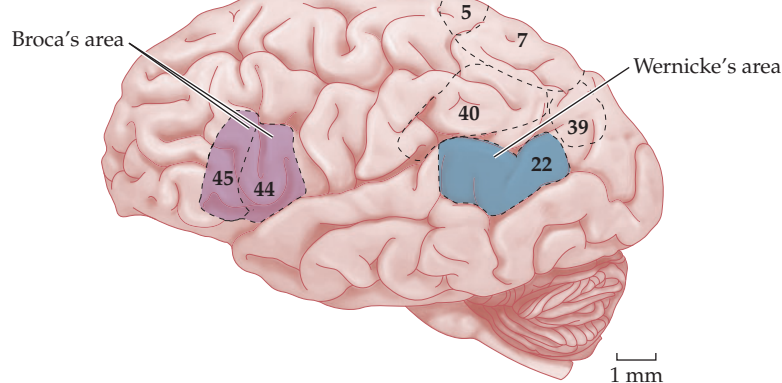


Figure 15.24 Vocal communication–related cortical areas in macaques and humans Areas 44 and 45 in the macaque (A) correspond to Broca's area in humans (B), whereas the temporal parietal junction (Tpt) in macaques has apparently been elaborated as Wernicke's area in humans. Areas 39 and 40 in the human parietal lobe have no homologue in macaques, although some investigators contend that lateral area 7 in the macaque is homologous with these areas. (A after Preuss and Goldman-Rakic 1991; B after Petrides et al. 2005.)